Peracarid fauna (Crustacea, Malacostraca) of the Northeast Water Polynya off Greenland: documenting close benthic-pelagic coupling in the Westwind Trough

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ABSTRACT: Composition, abundance, and diversity of peracarids (Crustacea) were investigated over a period of 3 mo in the Northeast Water Polynya (NEW), off Greenland. Samples were collected from May to July 1993 during expeditions ARK IX/2 and 3 using an epibenthic sledge on RV 'Polarstern' Within the macrobenthic community peracarids were an important component of the shelf fauna and occurred in high abundance in this area together with polychaetes, molluscs and brittle stars. A total of 38 322 specimens were sampled from 22 stations. Cumacea attained the highest total abundance and Amphipoda the highest diversity. Isopoda were of medium abundance, Mysidacea less abundant, and Tanaidacea least abundant. In total 229 species were found. Differences in composition, abundance and diversity do not reflect bathymetric gradients, but mainly the availability of food (phytoplankton and especially ice algae) and, hence, the temporal and spatial opening of the polynya. Thus primary production and hydrographic conditions (lateral advection due to the anticyclonic gyre around Belgica Bank) are the main biological and physical parameters influencing the peracarid crustacean community, documenting a close coupling between primary production and the benthic community in the eastern Westwind Trough. The high abundance of Peracarida, which are also capable of burrowing in the upper sediment layers, indicates their importance for benthic carbon cycling.

KEY WORDS: Crustacea · Peracarida · Greenland · Northeast Water Polynya · Abundance · Diversity · Benthic-pelagic coupling

INTRODUCTION

The hydrography of the northeastern Greenland Sea is strongly influenced by the cold polar water flowing from the Arctic Ocean along the Greenland coast to the south (Machoczek 1989, Birgisdottir 1990). The environmental conditions are characterized by very low, but relatively constant, water temperatures, long periods of ice cover, large seasonal fluctuations in light regime and, hence, generally only low biological activity (Hempel 1985). However, recent investigations have shown that benthic communities can be surprisingly rich in both biomass and diversity at various locations on the Greenland Shelf, as well as on the continental and mid-ocean ridge slopes (Piepenburg 1988, Svavarsson et al. 1990, Brandt 1993, Brandt & Piepenburg 1994, Piepenburg & von Juterzenka 1994). These communities are thought to be maintained by the temporarily high surplus of sympagic and/or pelagic production associated with nearby marginal ice zones of the East Greenland Current or of polynya regions.

Direct observations of seasonally sedimented fresh phytodetritus in the deep sea have been made (Billett et al. 1983) and primarily pulsed sedimentation events of organic material from the ice edges or open water to the bottom have been postulated (Hebbeln & Wefer 1991). The seasonal input of organic carbon has a direct effect on benthic communities (Suess 1980, Grebmeier et al. 1988, Graf 1989, 1992, Carey 1991). The bulk of suspended matter is accumulated in the benthic nepheloid layer (BNL) and advected, mostly by topographically driven currents in certain depth zones, to the areas of eventual deposition (Wainwright 1990, Graf 1992).

To assess the hypothetical relationship between quality and quantity of sedimentation and benthic response, a mesoscale study was undertaken in the Northeast Water (NEW) Polynya (Deming 1993, Hirche & Kattner 1994). The study was carried out by an international team, part of which was a group working for a multidisciplinary research programme (Sonderforschungsbereich 313 of the University of Kiel). A major objective of our programme is to assess the interrelationships between benthic community patterns and particle flux between sea floor, sediment-water interface and near bottom BNL (Graf 1992). Benthic and
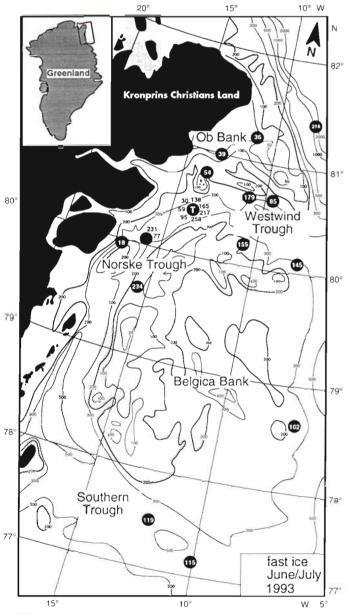

Fig. 1 Schematic illustration of the Northeast Water Polynya with the approximate positions of the stations sampled during 'Polarstern' ARK IX/2 and 3. T: time series stations

epibenthic mega- and macrofaunal organisms may play an important role in this feedback system although their abundance is lower than that of meiobenthos. Nonetheless, the impact of these animals on the microscale environment through bioturbation, bio-irrigation, habitat diversification, etc., is substantial (Gage & Tyler 1991, Romero-Wetzel & Gerlach 1991, Barthel 1992). However, the smaller macrofauna have been neglected in the methodological approach of many previous investigations, mainly because of small sample sizes and high diversity of taxa: until now most investigations on smaller peracarids were done on the basis of box-core samples, which cover only 0.25 m^2. As peracarids have quite a patchy distribution, depending on food availability (Brandt 1993), this device does not produce an accurate sample of the animals occurring in an area. Moreover, due to the wave preceding the box corer, many of the light animals on the surface of the sediment are swept away before the box corer hits the bottom.

Epi- and suprafaunal peracarid crustaceans, in terms of abundance and burrowing behaviour of many species, are presumed to contribute significantly to biogenic modification (bioturbation, bioresuspension) and particle flux in the benthic realm (Brandt 1993, Svavarsson et al. 1993). The peracarid crustaceans Amphipoda, Cumacea, Isopoda, Mysidacea and Tanaidacea are common and important macrobenthic animals occurring from shallow habitats to the abyssal plains of the world oceans in high abundance and diversity (Grassle & Maciolek 1992). The present study on composition, abundance, and diversity of peracarid crustaceans aims to investigate what influence the polynya has on the epibenthic peracarid community.

MATERIALS AND METHODS

Study area. The NEW Polynya refers to a more or less ice-free area south of Kronprins Christian Land (Nordostrundingen) on the east coast of Greenland (Fig. 1), and is regarded as the northernmost of a number of polynyas occurring along this coast (Vinje 1970, 1984). Waters south of Nordostrundingen open annually and have been reported to do so since at least the beginning of the present century (Koch 1945). The NEW Polynya can cover 40 000 to 44 000 km^2 (Wadhams 1981, Parkinson et al. 1987, Schneider & Budéus 1994). It begins to open in April or May, persists throughout the summer and starts closing in September. Originally it was assumed that the NEW Polynya was a latent heat polynya (Smith et al. 1990), where warmer waters in the deeper layers of the NEW Polynya possibly contribute to its opening (Wadhams 1981). Recent investigations, however, indicate a

northward flow, part of an anticyclonic gyre around Belgica Bank (Bourke et al. 1987, Schneider & Budeus 1994, Rumohr pers. comm.), instead of an overall southward circulation along the coast. The NEW Polynya mainly covers the northern part of Belgica Bank. The latter has a complicated topography. Its structure is dominated by a trough system (Belgica Trough, Westwind Trough and Norske Trough; Fig. 1) around the central bank. On the banks depths can be as shallow as 60 m, in the trough system more than 300 m, but rarely exceeding 500 m (Schneider & Budéus 1994). To the north the NEW Polynya is bordered by Kronprins Christian Land, Nordostrundingen and the Ob Bank. The northern Greenland continental shelf is narrow. The western part of the NEW Polynya extends into 2 valleys, the northern Ingolfsfjord and the more southerly Dijmphna Sund. South of these over the Norske Trough at about 79° N, a distinct extension of fast ice is present, possibly grounded in the extremely shallow surroundings on the Belgica Bank (Schneider & Budéus 1994).

A strong vertical density gradient exists between the 2 main water layers. The upper cold, fresh Polar Water (PW) (Bourke et al. 1987, Budéus et al. 1993) extends to about 100 m depth and is characterized by a salinity of 34.4 (Hopkins 1991). Underneath this layer the water is slightly warmer and more saline. A gradual rise in temperature and salinity occurs with increasing depth to about 0.7 to 0.8°C and 34.8 respectively (Fig. 4 in Schneider & Budéus 1994). Conditions below 300 m are almost homogenous (Schneider & Budéus 1994). This fairly stable vertical layering is probably due to both melting of sea ice and runoff from land. Schneider & Budéus (1994) postulate development of plankton blooms, especially in the northern part of the NEW Polynya. Recent work on board the German research vessel 'Polarstern' revealed that pelagic and benthic biomass were higher in the polynya than in the surrounding area (Hirche & Bohrer 1987, Piepenburg 1988, Hirche et al. 1991, this study).

Sampling. Material was collected in the NEW Polynya (Fig. 1) off Greenland during RV 'Polarstern' expeditions ARK IX/2 and 3 from May to late July 1993 (for exact data see station list, see Table 1). We employed an epibenthic sledge (EBS) (Rothlishberg & Pearcy 1977), modified after Buhl-Jensen (1986) and Brattegard & Fosså (1991). This carries a sampling box in the middle of the frame. The opening is 100 cm wide and 33 cm high and extends from 27 to 60 cm above the bottom. A plankton net of 0.5 mm mesh size is attached, the cod end of which is enclosed by a 0.3 mm mesh net. When the sledge touches bottom, a shoe fixed to the box door opens the door. The door is closed by means of springs when the sledge leaves the sea floor. In addition to the EBS, a CTD, Agassiz trawl, box

corer, multicorer, bottom-water sampler and bongo net were employed at almost all stations where the EBS was used. The deployment of this gear provided measures of environmental parameters, which helped to explain the variation in abundance and diversity at the different stations (Ahrens 1994, Ritzrau 1994, Graf & Scheltz pers. comm.).

Although the sledge was designed to sample the water column just above the sediment, observations by scuba divers have revealed that water below the opening is also sampled because of turbulence in front of the gear (Buhl-Jensen 1986). This explains the high percentage of epifauna, which constitute the bulk of the samples.

Usually the sledge was hauled over the ground for 10 min at a mean velocity of 1 knot. The haul distances were calculated on the basis of the GPS-derived positions of the ship at the start and end of the haul as:

$$\text{Distance (m)} = 1852\sqrt{(\Delta \text{lat}')^2 + (\cos \text{lat} \times \Delta \text{long}')^2}$$

(after Brattegard 1993, Brandt pers comm.).

Area swept was calculated by multiplying the distance travelled by the area of the box opening. As the distances sampled varied from 289 to 489 m (Table 1), numbers of specimens and species were calculated for a standardized 1000 m haul (Table 2) (Basford et al. 1989, Svavarsson et al. 1990, Brandt 1993). Positions of EBS sampled stations are shown in Fig 1 and Table 1. The time series stations (T) were visited 7 times at approximately 10 d intervals during the 3 mo. The EBS catches at Stns 30 and 59 (both T-stations) were not quantitative. The qualitative data are considered in the results (see Tables 2 & 3) but not presented in figures or station analyses.

When the sledge reached the deck of the vessel, samples were suspended, decanted through a 0.3 mm screen and preserved in 4% buffered formaldehyde solution. After 3 d the samples were washed and transferred into 70% ethanol. For comparison of fauna from the 22 stations the complete samples were analysed.

Data analysis. The abundance and diversity data of the peracarid crustacean species caught are summarized in Tables 2 & 3. For differentiation of distinct species assemblages at stations, according to the pattern of their co-occurrences (R-mode), an explorative statistical approach as proposed by Field et al. (1982) was applied. The multivariate data set was subjected to both classification and ordination analyses, i.e. agglomerative hierarchical cluster analysis (Romesburg 1984, Piepenburg & Piatkowski 1992) and non-metric multidimensional scaling (MDS; Kruskal & Wish 1978, Wilkinson 1987), respectively.

The Bray-Curtis coefficient (Bray & Curtis 1957) was used as a parameter of species distribution resem-

Table 1 Station list of RV 'Polarstern' expeditions ARK IX/2 and 3 to the Northeast Water Polynya. T: time series station; [a]Ritzrau (1994) after Ahrens (1994); [b]Ahrens (1994); –: not measured. Dates given as Day.Month.Year

Station:	18	T 30	36	39	54	T 59	77	85	T 95	102	115
Date	27.05.1993	30.05.1993	03.06.1993	04.06.1993	07.06.1993	08.06.1993	12.06.1993	14.06.1993	17.06.1993	20.06.1993	30.06.1993
Latitude (N)	79°54.78'–79°54.63'	80°25.29'–80°25.27'	81°15.30'–81°13.27'	81°00.93'–81°00.73'	80°44.84'–80°45.06'	80°29.65'–80°29.88'	80°04.73'–80°04.55'	80°35.34'–80°35.19'	80°27.11'–80°27.00'	78°38.41'–78°38.28'	77°10.00'–77°09.80'
Longitude (W)	16°58.29'–16°58.70'	13°47.44'–13°48.65'	11°30.44'–11°30.65'	12°56.82'–12°55.91'	13°42.27'–13°42.59'	13°41.83'–13°41.65'	15°44.04'–15°44.23'	09°18.58'–09°17.61'	13°25.24'–13°24.12'	06°59.47'–06°59.00'	10°28.20'–10°28.80'
Depth (m)	310	334	45	50	174	305	425	270	315	232	492
Distance run (m)	366	349	339	469	443	452	361	413	357	351	490
Surface water temp. (°C)	-1.45	-1.6	-1.29	-1.1	-0.8	-0.8	-0.96	-1.5	-0.9	-1.1	-1.48
Salinity (psu)	–	–	–	–	–	–	–	–	–	–	32.13
Bottom water temp. (°C)[a]	–	–	–	–	–	–	–	–	0.668	–	0.801
Current velocity (cm s⁻¹)[a]	–	–	–	–	–	–	–	–	0.4	–	26
Sediment	High % of sand Many dropstones	Soft mud	Coarse sediment Low water content	Soft mud	Soft mud/clay	Soft clay	Very soft mud	–	–	–	Very soft mud
% of sand (+)	–	–	10	6	10	20	–	–	10	–	1
% of silt (+)	–	–	89	93	84	78	–	–	88	–	97
Foram. >63 μm (ind. 10cm⁻³)[b]	–	117	155	364	177	507	–	–	236	–	172

Station:	119	T 138	145	155	T 165	179	216	T 217	231	234	T 258
Date	09.07.1993	05.07.1993	08.07.1993	11.07.1993	12.07.1993	14.07.1993	19.07.1993	19.07.1993	22.07.1993	22.07.1993	26.07.1993
Latitude (N)	77°43.24'–77°43.09'	80°29.92'–80°29.10'	80°01.73'–80°01.65'	80°06.89'–80°06.86'	80°28.06'–80°27.88'	80°36.56'–80°36.38'	81°12.65'–81°12.45'	80°27.28'–80°27.29'	80°04.27'–80°04.27'	79°56.47'–79°56.27'	80°27.01'–80°26.85'
Longitude (W)	14°07.32'–14°07.61'	13°38.18'–13°36.90'	06°44.65'–06°43.55'	10°41.71'–10°42.62'	13°36.64'–13°37.06'	11°17.20'–11°17.98'	08°42.21'–08°42.69'	13°33.87'–13°33.02'	15°45.59'–15°45.83'	15°02.37'–15°02.25'	13°36.85'–13°36.70'
Depth (m)	377	314	310	186	320	260	517	328	411	180	326
Distance run (m)	338	383	339	308	406	431	420	289	305	388	308
Surface water temp. (°C)	-1.3	0.13	0.6	-1.4	4.3	-0.18	1	1.4	1.3	0.6	-0.13
Salinity (psu)	–	–	31	30.96	32.35	31.39	–	–	–	32.42	32.16
Bottom water temp. (°C)[a]	1.075	0.686	0.422	-0.182	0.52	0.373	–	0.516	–	–	0.602
Current velocity (cm s⁻¹)[a]	23.5	8.5	7.1	21	14.9	6.5	–	6.4	–	2.9	10.4
Sediment	Soft mud	Soft mud	Coarse sediment	Soft mud	Soft mud/clay	Soft clay Many big stones	–	Soft mud/clay Some big stones	Very soft mud	Fine, soft mud Small stones	Very soft mud Some stones
% of sand (+)	4	–	10	6	10	20	–	9	4	28	11
% of silt (+)	96	–	89	93	84	78	–	86	95	67	69
Foram. >63 μm (ind. 10cm⁻³)[b]	166	117	155	364	177	507	–	141	139	424	291

blance, both for classification and ordination. The multivariate pattern in terms of station similarities was depicted by dendrograms for cluster analysis and ordination biplots for multidimensional scaling. Based on discontinuities recognized in these graphical representations of the overall resemblance patterns distinct species assemblages were arbitrarily differentiated and marked. For the computation of similarities between any 2 clusters the Unweighted Pair-Group Method using Arithmetic Averages (UPGMA) was used.

Station parameters were computed for each station from the NEW Polynya. In Table 4 the dominant species with their maximal dominance, and the real and cumulative numbers of species at stations are given and calculated diversity and evenness indices are shown. Abundance and constancy of peracarid species at the stations was parameterized by certain measures such as median and range of numbers of individuals per catch, percent dominance, and frequency of occurrence.

The term species diversity is used to mean species richness, i.e. the number of species sampled at a station (Hurlbert 1971). For comparisons of diversity patterns of the samples, the Shannon-Wiener index of diversity (H') (Shannon & Weaver 1949) was calculated for each station. H' is dependent on sample size. Because there were great differences in the sample sizes in this investigation, sample size was standardized; moreover, the index was supplemented by rarefaction curves (after Sanders 1968) for all stations in order to compare the expected number of species in equally large samples. Soetart & Heip (1990) describe the dependence of the diversity indices on the sample sizes, which is more pronounced in highly diverse environments. However, there is no doubt that the sample size at the stations is large enough for this study (Table 2).

Table 2. Abundance and species diversity of peracarid crustaceans sampled from stations in the NEW Polynya. Values are no. of species/no. of individuals found per 1000 m EBS trawled distance; T: time series station. Depths in m

Stn	Amphipoda	Cumacea	Isopoda	Mysidacea	Tanaidacea	Depth
18	26/999	13/493	27/1814	4/104	3/153	310
30T	3/12	2/6	4/12	–	1/6	330
36	27/2457	6/1871	7/632	–	2/29	45
39	29/5687	9/58	8/422	1/21	1/41	50
54	27/963	11/365	9/268	3/200	3/12	174
59T	1/2	1/2	3/10	–	1/2	300
77	25/494	9/244	19/1801	4/551	4/53	425
85	33/1055	7/1216	19/1201	4/1178	3/43	270
95T	42/1535	12/3194	21/3664	4/904	3/113	315
102	44/1812	13/1644	26/1256	3/6165	4/92	232
115	16/140	8/91	15/180	2/111	3/10	492
119	16/199	9/51	9/189	5/353	1/6	377
138T	37/1357	11/2991	23/1424	5/407	3/69	314
145	35/7399	12/1630	20/1205	4/478	4/33	310
155	44/3666	13/3798	20/1256	4/1521	4/1799	186
165T	39/791	10/3678	21/3384	5/1625	4/132	320
179	35/4876	12/6304	26/3465	5/1067	4/128	260
216	6/32	8/63	13/124	5/81	3/12	517
217T	29/945	8/1778	20/1400	5/1773	2/41	328
231	31/1816	11/681	19/1667	6/576	6/282	411
234	31/995	13/1585	23/458	2/883	4/82	180
258T	45/868	9/1651	24/1965	5/940	1/94	326
Total	130/31438	31/34377	52/27797	8/13389	8/3322	

Total no. of species/individuals: 229/110323

RESULTS

The exact number of specimens analysed was 38 322. These were 229 species belonging to 121 genera and 51 families (Table 3). In the part of the NEW Polynya sampled during our cruise 229 species of peracarid crustaceans were found (Tables 2 & 3). These species comprise a total of 110323 individuals at all stations (including the non-quantitative Stns 30 and 59) when standardized for 1000 m hauls (Table 2). Stns 30 and 59 were excluded in further analyses as the EBS was blocked by stones.

Among the Peracarida, Cumacea were most frequent (33.1%), followed by Amphipoda (31.4%), Isopoda (21.6%), Mysidacea (10.6%), and Tanaidacea (3.3%) (Tables 2 & 3). Amphipoda, however, were most diverse and comprised 130 species (57%). Isopoda were second in diversity (22.6%), followed by Cumacea (13.5%), and Mysidacea and Tanaidacea (3.5% each) (Table 3). The most abundant family sampled was the Diastylidae (Cumacea), and *Leptostylis villosa* was the dominant peracarid species in the polynya (Table 4). Stn 179 showed the highest abundance of

Table 3. Overview of diversity of the peracarid taxa in the NEW Polynya

	Amphipoda	Cumacea	Isopoda	Mysidacea	Tanaidacea	Total
Families	28	5	16	1	1	51
Genera	68	10	31	6	6	121
Species	130	31	52	8	8	229
Specimens	31438	34377	27797	13389	3322	110323

Table 4. Station parameters of the NEW Polynya, with most dominant species. Sum: sum of individuals of each station; Max. dom.: % dominance of the dominant species of the station; S: number of species at each station; E(S): estimated number of species calculated with the rarefaction method of Sanders (1968) for a standardized abundance; H': diversity index of Shannon = $-\sum(n/N)\ln(n/N)$; Pielou: evenness index of Pielou (1966) = $H'/\ln(S)$

Stn	Sum	Max. dom.	Dominant species	S	E(S)	H'	Pielou
18	3563	17.2	*Halirages fulvocinctus*	73	10.1	3.322	0.779
36	4989	12.7	*Monoculodes* sp.	42	8.6	2.695	0.726
39	7228	24.9	*Westwoodilla megalops*	48	8	2.613	0.695
54	1808	25.2	*Bathymedon* sp.	53	8.6	2.854	0.726
77	3143	38	*Eurycope brevirostris*	61	8	2.708	0.659
85	4693	24.5	*Erythrops erythrophthalma*	66	8.5	2.834	0.689
95	9410	16.4	*Eurycope brevirostris*	82	9.7	3.221	0.737
102	5420	15.8	*Brachydiastylis nimia*	90	9.9	3.279	0.734
115	532	19.1	*Gnathia stygia*	44	9.2	2.976	0.796
119	798	21.1	*Erythrops glacialis*	40	8.7	2.84	0.775
138	6248	19.7	*Leptostylis villosa*	79	9.6	3.216	0.745
145	4085	16.1	*Eurycope brevirostris*	75	9.6	3.143	0.733
155	12040	13.5	*Leucon nasica*	85	9.4	3.118	0.711
165	9610	13.9	*Leptostylis villosa*	79	9.5	3.124	0.719
179	15929	14.7	*Bathymedon* sp.	82	10.1	3.281	0.747
216	312	12.1	*Pseudomma frigidum*	35	9.9	3.089	0.876
217	5937	15.7	*Pseudomma frigidum*	64	9.9	3.199	0.775
231	5022	13.4	*Eurycope inermis*	73	10.6	3.447	0.809
234	3929	22.1	*Erythrops erythrophthalma*	73	9.5	3.138	0.734
258	5518	14.5	*Eurycope inermis*	84	10	3.324	0.754
Total	110214 [a]	7.5	*Leptostylis villosa*	229	11.7	4.037	0.744

[a] Stns 30 and 59 excluded

Peracarida (Fig 2a). Total diversity was highest at Stns 102, 155, and 258 (Fig. 2b) but was also quite high at some other stations. The abundance of cumaceans and isopods was higher than that of amphipods at many stations in the NEW Polynya (Table 2); however, at Stn 39 amphipods were predominant. In terms of relative diversity, amphipods were most diverse at 18 stations, and only at Stns 115 and 216 (deep stations) were the Isopoda more diverse (Table 2).

The northernmost station (216) was also the deepest (517 m) and showed the lowest abundance and diversity of peracarid taxa. Stns 115 and 119 were the southernmost stations and were still relatively deep (377 to 492 m). The abundance and diversity values at these 2 stations were both low, suggesting that depth may be a controlling factor. However, Fig. 3 shows that there was no correlation of abundance or diversity with depth and, therefore, factors other than depth must be involved. Although there are no significant relationships between depth and diversity, some taxa do show patterns (A. Brandt, S. Vassilenko, D. Piepenburg & M. Thurston unpubl.). Amphipod numbers and diversity (based on proportional representation in samples) are significantly higher (Spearman's rank correlation coefficient) at shallow depths, whereas the reverse is true for isopods and mysids.

Both abundance and diversity were highest at stations sampled around 300 m depth, especially in the Westwind Trough in the north of the polynya (Fig. 2b). Fig. 4a, b shows the dendrogram of a cluster analysis of the stations on the basis of the peracarid distribution. Stn 54 does not fit very well with Stns 115, 119 and 216 and has a more random position as illustrated in the MDS plot (Fig. 4b). Stns 115, 119 and 216 are the deepest stations and also show the lowest abundance values, which is most probably correlated with the low availability of nutrients and the low productivity of the water masses due to both ice cover and hydrography (e.g. circulation pattern). Although Stn 234 is similar in species composition to 179 and 155 (Fig. 4a, b), it is located much further away and the species assemblages there must be influenced by other forces than at Stns 179 and 155.

Stn 102 was situated on the eastern Belgica Bank (Fig 1), between the stations of the Belgica Dyb and the Norske and Westwind Troughs, where most stations were located. This station showed abundance values between those of the southern stations (115 and 119, very low abundances) and, for example, those of the time series stations of Stns 179 and 155, which showed extremely high values. Abundance values were highest for Stn 179, which might be due

to the current direction and the accumulation of organic matter resulting from lateral advection, which is similar, but a little less pronounced, at Stn 155. Stn 145 was located at the northeastern edge of AWI Bank (ca 80° N, 08° W), close to the influence of the cold Arctic water; this station also shows low abundance values. Stns 36 and 39 were shallowest (about 50 m), situated close to the fast-ice margin off Kronprins Christians Land. Here, sediments contained a higher percentage of sand than at the other stations, as seen on the surfaces of box corers from the same locality (Ahrens 1994). The amphipod abundance of these stations is somewhat higher than at the time series stations; however, the total peracarid abundance is much lower than at Stns 179 and 155. Stns 18 and 234 were situated in the East Greenland Coastal Current, close to the southern area of fast-ice, which covers part of the Norske Trough. This water probably transports relatively low amounts of nutrients in this area, as it flows mainly under the ice. These 2 stations and Stns 77 and 231, which are nearby, showed low abundance. Interestingly, Stn 85 also had a relatively low abundance despite its proximity to Stn 179, where the highest level of abundance was recorded. The time series stations and Stns 54, 179 and 85 lie in the outflow from the northern Ingolfsfjord, which is significant in terms of community patterns (Brandt et al. unpubl.) The more southern Dijmpha Sund may have some influence on Stns 18, 77, and 231.

Fig. 2. (a) Total abundance and (b) total diversity of all peracarid taxa at 20 stations in the Northeast Water Polynya

DISCUSSION

In contrast to megafaunal organisms, macrobenthic peracarid crustaceans are too small for *in situ* analysis by camera or video systems (e.g. Hargrave 1985, Smith 1985, Piepenburg 1988, Hecker 1990, Gutt 1991, Piepenburg & von Juterzenka 1994), and are rarely abundant enough to be sampled adequately by quantitative samplers, such as box corers. Traditionally box cores cover areas of 0.25 m². Such samples cannot provide unbiased abundance estimates for species which might occur in low densities (e.g. Tanaidacea), swarms (Mysidacea), or have a patchy distribution due to food availability (all Peracarida) (Holme & McIntyre 1984).

'Winnowing' by the box may also influence the sample efficiency to an unknown degree. The best method for catching greater amounts of these taxa is the use of towed gear, such as the epibenthic sledge (modified after Rothlishberg & Pearcy 1977), despite potential avoidance reactions by the more mobile organisms such as mysids or some amphipods. Towed gear has been frequently used in the past to catch peracarids even though, depending on the smoothness of the ground, it may not always work with exactly the same efficiency (e.g. Buhl-Jensen 1986, Svavarsson et al. 1990, 1993, Brattegard & Fosså 1991). Nevertheless, the EBS is still the best instrument to sample small peracarids. Replicates using this gear at the same stations

a

Depth-abundance relation
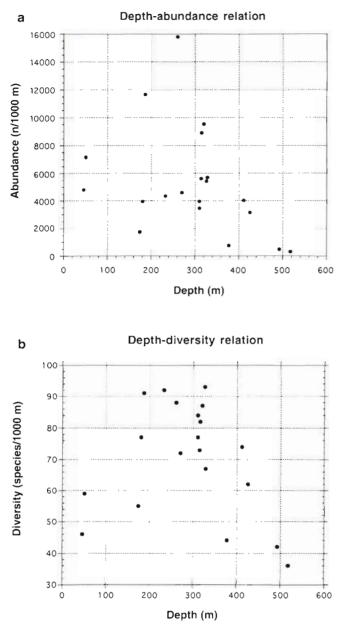

b

Depth-diversity relation

Fig. 3. Relation between (a) depth and abundance and between (b) depth and diversity at 20 stations sampled in the polynya (for exact depth of stations see Table 1)

proved to be as variable as those among different stations; therefore Brattegard & Fosså (1991) suggest taking only 1 sample at each station. In the NEW Polynya, the sledge is usually towed at 1 knot, and mysids and amphipods are caught in considerable numbers (Tables 2 & 3).

The high biodiversity in the NEW Polynya described for Peracarida (229 species) implies that the environmental conditions (e.g time of opening and closing of the polynya) must have been relatively stable over a long period of time northeast of Greenland. Intense

melting of ice and subsequent changes in seawater salinity might strongly disturb the benthic community (not only of peracarid crustaceans) in this area and, hence, affect the biological balance of this ecotope.

The cluster analysis of the stations (Fig. 4) revealed that, generally, stations which lay very close together (it was attempted to take the samples at exactly the same locality; Ahrens 1994, p. 69) also showed the highest resemblance (time series stations 95, 138, 165, 217, and 258), which might indicate that seasonal variability (samples taken over a period of more than 2 mo) is not as important as geographical position of the stations. Stns 179 and 155 in the Westwind Trough were very similar to the time series stations with regard to species composition, but abundance values were higher.

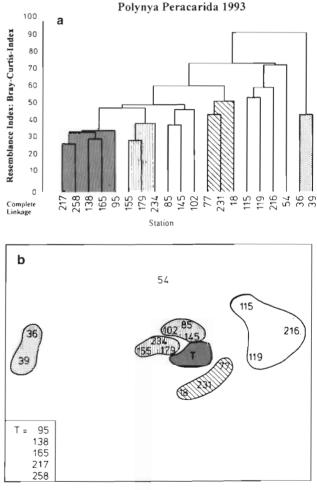### Polynya Peracarida 1993

a

b

Fig. 4. (a) Dendrogram from the cluster analysis and (b) plot of the multidimensional scaling (2 dimensions) of the EBS samples taken in the Northeast Water Polynya from May to August 1993 (fourth root transformation of species abundance values; Bray Curtis Index as resemblance measure; complete linkage strategy, cophenetic index 0.9389); stress of MDS solution 0.092

Very few publications on faunal composition of peracarid taxa contain data comparable with the polynya data reported here. Buhl-Jensen (1986), also employing the same construction of an EBS, registered 159 amphipod species from the Norwegian continental shelf (60 to 67° N). In the NEW Polynya, which is much further north and affected predominantly by cold Arctic polar water of the East Greenland Current, 130 amphipod species were sampled. Svavarsson et al. (1993b; compare also Svavarsson et al. 1990) listed 106 Arctic and Arctic-boreal species of asellote isopods (these are among the most predominant animals of the deep sea and polar fauna) in the Norwegian, Greenland, Iceland, and North Polar Seas. Only 69 of these listed species had been reported from the depth range 0 to 517 m (Stn 216, the deepest station sampled in the polynya). In the NEW Polynya 42 of the 69 species have been recorded in our study. This represents two-thirds of all known Arctic-boreal and Arctic asellote isopods, suggesting that the EBS has a high catch efficiency and the fauna of the NEW Polynya are highly diverse. The number of asellotes found in the polynya is extraordinarily high if one takes into consideration that these findings refer to 22 stations, while those of Svavarsson et al. (1993b), who also referred to EBS samples in their recent investigations, and literature data have accumulated over the past 100 yr. On a smaller scale, differences between the northern and southern area of the NEW Polynya are pronounced, especially with regard to abundance of peracarid taxa, as well as between banks and troughs in general. Generally the banks are dominated by coarse sediments with many smaller stones or rocks which are inhabited by sessile suspension feeders, sponges, alcyonarians, and soft corals. In general the larger megabenthic animals, ophiuroids, starfishes, pycnogonids, bivalves, etc. dominate at these stations. However, the slopes of the banks and the bottoms of the troughs are characterized by soft sediments, with a lower number of megabenthic animals. At these stations the importance of smaller macrobenthic taxa, especially peracarid crustaceans and polychaetes (K. Schnack pers. comm., K. Schnack & A. Brandt unpubl. data from box corer analyses taken at the same stations), increased. These differences can be due to either different current regimes (stronger or weaker current velocities, direction, etc.) (Künitzer et al. 1991), or different sedimentation patterns (Grebmeier et al. 1988, 1989, Basford et al. 1990, Jensen et al. 1992), sediment erosion by hydrodynamic forces, or other abiotic parameters, such as temperature and salinity (Dyer et al. 1983). Similar to the present results for the peracarid abundance in the NEW Polynya, Ambrose & Renaud (1995, their Fig. 3) found much higher densities of polychaetes in the troughs, especially in the north and northeast of

the NEW Polynya, compared to the Southern Trough. They attributed this to grazing of herbivorous copepods, which is about 3 times higher in the south (Ashjian et al. 1995). Ambrose & Renaud (1995) found no relationship between water-column and benthic pigment concentration (the most important predictor of infaunal density and polychaete biomass) in the Southern Trough, although phytoplankton standing crops were similar to those in the Northern Trough (Smith et al. 1995). In their opinion this might indicate that water column and benthos were decoupled in the south, possibly due to the abundance of grazing phytoplankton. Pomeroy (1974) and Jumars et al. (1989) suggested that grazers are needed to stimulate bacterial activity (by providing substrate of high quality); the grazers should enhance the role and importance of the microbial loop in processing carbon. This hypothesis, however, does not prove true for the NEW Polynya, because in the Northern Trough heterotrophic activity of bacteria in the BNL was generally higher than in the Southern Trough (Belgica Dyb) (Ritzrau 1994, p. 96–99). On the other hand the lower numbers of phytoplankton in the Northern Trough might reduce carbon cycling in the water column and result in a more efficient transfer of carbon from the pelagial to the benthos.

The diversity of Peracarida in the polynya area turned out to be much higher than had been expected, especially if we consider recent discussions on decrease of diversity with latitude (e.g. May 1992, Gage & May 1993, Poore & Wilson 1993, Rex et al. 1993, Brey et al. 1994). However, such arguments are based on surveys deeper than 500 m, whereas stations in the NEW Polynya were situated on the continental shelf — some were almost 500 m deep, the deepest (Stn 216) was 517 m. Nevertheless, no obvious correlation of abundance or diversity with depth could be found (Fig. 3a, b). At our stations diversity was highest around 300 m depth (Fig. 3b). Isopoda were more diverse than Amphipoda in the deeper stations (115 and 216), which might indicate an increasing importance of Isopoda within the peracarid community with depth (Table 2). Brey et al. (1994) cautioned against general statements, such as a decrease of deep-sea diversity with latitude. Our findings in the NEW Polynya also suggest that, rather than over-emphasizing a single parameter (such as latitude) and neglecting the others a variety of different biotic and abiotic parameters must be considered to explain species communities. Moreover, studies of biodiversity at high latitudes have been performed infrequently until now, and investigations in the Antarctic have already falsified the hypotheses of Rex et al. (1993) (Brey et al. 1994).

General discussions on diversity (e.g. Sanders et al. 1965) also have to be considered, as lateral advection and plankton and ice-algae blooms might not be the

only effects influencing peracarid community composition. The polynya area is open for only 4 to 5 mo per year, and, hence, is far from being uniform. However, biological disturbance processes (Dayton & Hessler 1972, Smith & Hamilton 1988), competition (Grassle & Sanders 1973), habitat heterogeneity (Jumars 1976), and competition and predation correlated with production (Rex 1976), or small-scale disturbance within stable communities (Grassle & Morse-Porteous 1987) might be biological factors which could well influence the communities characterized for the different stations. These biological inter-species relationships and effects might be more important during the winter months, when little or no organic matter reaches the seafloor or remains from summer deposition.

Peracarids, such as epifaunal isopods, which can burrow in the first centimeter of the sediment (e.g. Ischnomesidae, Eurycopidae, Ilyarachnidae, Desmosomatidae) (Hessler & Strömberg 1989) and are mainly deposit feeders, have an important influence on niche diversification, bioturbation effects, and benthic carbon cycling (Brandt 1993, Brandt & Piepenburg 1994). As peracarid crustaceans are known to increase in importance with depth (Dahl et al. 1976, Grassle & Maciolek 1992), it might be expected that a vertical transect of the East Greenland shelf would reveal highly diverse peracarid communities, even at deeper stations. This question will be answered in future papers (author's unpubl. data from expedition ARK X-1 with RV 'Polarstern' at 75° N, July–August 1994).

The surface and bottom water temperature was slightly lower at the southern stations (115 and 119) compared with the stations of the Norske and Westwind Troughs (Ritzrau 1994, p. 96; compare Ahrens 1994, p. 108). However, these slight temperature differences most probably do not explain the higher abundance in the north since temperature changes within a range of ± 1 to 2°C do not affect the life of these taxa, as was observed in peracarids (e.g. *Anonyx nugax*, *Paramphitoe hystrix*) kept alive in aquaria for some time. Neither were differences in salinity pronounced between the stations (compare Machoczek 1989); the presence of peracarids thus cannot be affected by this parameter either. In aquaria the animals were able to tolerate changes in salinity of 2 to 3‰ (A. Brandt unpubl.). The differences in the sediment surfaces on banks and in troughs can probably be attributed to higher current velocities on the banks in comparison to the troughs. This could explain differences in abundance of peracarids between bank and trough stations (the amount of fine organic matter available for feeding of peracarids might be lower in areas of higher current velocities); however, it does not explain differences between southern and northern trough stations. Investigations of chlorophyll *a* and

ATP contents of the upper sediment layer do not explain these differences (Ahrens 1994, p. 53, 108; Graf & Scheltz pers. comm.). Only at Stn 179 in the north did the highest values for the incorporation of chlorophyll into the sediment and for biological activity (ATP measurements; for methods see Graf & Linke 1992, Heip et al. 1992) correspond with the highest abundance values of Peracarida. The differences found for peracarids between northern and southern troughs of the polynya area resemble meiobenthic community patterns, as the Southern Trough (Belgica Dyb) is characterized by a distinct nematode community (R. Herman & P Jensen pers. comm.). The high values in peracarid abundance and in chlorophyll incorporation into the sediment found at Stn 179 might indicate the impact of epibenthic peracarids on bioturbation processes in this area (Grebmeier & McRoy 1989, Brandt 1993, Brandt & Piepenburg 1994). The incongruence in our findings concerning the lower abundance of peracarids in the south, where the chlorophyll incorporation and biological activity (ATP measurements) are not strikingly lower, might indicate a greater abundance of smaller meiobenthic organisms in the south, which could lead to a most rapid incorporation of organic matter into the sediment by bioturbation processes. On the other hand, Ambrose & Renard (1995) implicate a possible grazing effect of copepods for the lower densities of polychaetes in the southern trough (Ashjian et al. 1995, Smith et al. 1995). Grazing would also affect the availability of food for peracarids.

Peracarid crustaceans and other epi- and suprabenthic animals depend on organic material, which is accumulated in the near bottom water (BNL). Thus the content of organic matter (e.g. particulate organic carbon, POC) in the BNL must have a strong impact on the peracarid communities. Therefore it is not surprising that we found the highest values of peracarid abundance at stations where POC values in the BNL were highest (compare Ritzrau 1994, p. 96–99). At the southern stations (115 and 119) the POC content was not low; however, higher amounts of freshly sedimented organic material (especially chlorophyll equivalents) in the BNL were found in the Northern Trough, especially at the time series stations, and at Stn 179 we found the highest values (Ritzrau 1994).

CONCLUSIONS

These findings suggest the following interpretation: the water masses from the Arctic Ocean flowing south through the Fram Strait carry only a relatively low amount of nutrients, primary production being not yet possible because of the almost permanent ice cover. Water masses forming the East Greenland Current

flow south along the eastern side of Belgica and Ob Bank where the ice extent is still pronounced, especially in May, but also in June. Driven by the topography of the Belgica Dyb and the north-flowing coastal current off Greenland, these water masses deviate towards the mainland and form the anticyclonal gyre around Belgica Bank. Here, in the opening of the Belgica Dyb, the ice cover is almost permanent, Stns 115 and 119 (close to the Greenland continental slope) are situated in an area of almost constant ice cover, and only slight movements of the ice occur (Ritzrau 1994, p. 38, T. König pers. comm.). Primary production is hardly possible; and, due to lateral advection, blooms of algae at the ice edges probably do not affect the benthic communities.

In the northern part of the NEW Polynya, however, we find the highest values of POC (in terms of freshly sedimented material, chlorophyll equivalents) and peracarid abundance, probably resulting from a combination of hydrographic condition and primary and especially ice-edge production. The northern part of the polynya is broadest and open longest. Movement of the ice flows is very high in the north (König pers. comm.), which accelerates blooms of ice algae at the floes' margins. The effect of production in the water column is probably of minor importance, relative to the ice-algae blooms. If we assume a higher productivity in the northeast of the polynya and consider the northward movement of the East Greenland Coastal Current, it becomes obvious that the finding of the higher POC values can be explained by high sedimentation of organic matter (ice algae) and by lateral advection (accumulation of organic matter in the north). Assumption of these processes also implies that peracarid abundance should be lower at stations close to the ice edge (18, 234, 77, 231) (compare also schematic model of Ritzrau 1994, p. 60), and nearer the northern fast-ice extension (36, 39). Except for the Amphipoda at Stns 36 and 39, this did prove true (Table 2). The process of lateral advection might also explain the slightly higher values at Stn 179 compared with those at Stn 155, which also lies in the area of relatively low ice cover but on the southern slope of the Westwind Trough where the influence of the lateral advection might be slightly reduced.

The high biodiversity of Peracarida in the NEW Polynya, and also the presence of many juveniles and ovigerous females (Brandt et al. unpubl.) indicates high productivity of this area during summer months. Both abundance and biodiversity of peracarid communities in the NEW Polynya are influenced mainly by productivity (particularly ice algae) (Ritzrau 1994, Ambrose & Renaud 1995, Ashjian et al. 1995, Smith et al. 1995) and hydrography (lateral advection) (Ritzrau 1994, Schneider & Budéus 1994) during summer

months. In winter, when the polynya is closed, biological processes of interspecies relationships (such as competition and predation) likely control the composition of peracarids. The high abundance of peracarid crustaceans at Stn 179, where we also found a high concentration of chlorophyll equivalents (POC) in the BNL (Ritzrau 1994), chlorophyll incorporation into the sediment and biological activity (ATP content) of the upper sediment layer (Graf & Scheltz pers. comm.), could indicate that they have a high potential for bioturbation and resuspension and, hence, are important in benthic carbon cycling.

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