THE MACROFAUNA AND MAIN FUNCTIONAL INTERACTIONS IN THE SILL BASIN SEDIMENTS OF THE PRISTINE HOLANDSFJORD, NORTHERN NORWAY, WITH AUTECOLOGICAL REVIEWS FOR SOME KEY-SPECIES

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In order to study the sediment macrofauna (> 1 mm) in a pristine sill fjord system, baseline investigations were carried out in 1991, 1992 and 1994 in the 30 km long triple-basined Holandsfjord, Northern Norway. Three sampling stations were located in the deepest part of each basin and one in the outer margin of the fjord just outside the outer basin. The innermost basin has relatively high inorganic sedimentation rates caused by glacier-derived melt water run-off. The bottom sediments were generally clay-silt dominated with an organic carbon content between 7 and 11 mg g^{-1} in the sill basins and between 21 and 22 mg g^{-1} in the outer margin of the fjord. The Shannon-Wiener diversity index ranged between 3.0 and 4.2, the number of individuals between 373 and 4910 ind. m^{-2} and the number of taxa per station between 23 and 45. The highest diversity was found at the outer margin of the fjord while the highest number of taxa, in two of three sampling years, occurred at the fjord head. The fauna at the fjord head was numerically dominated by the subsurface feeding detrivorous polychaete *Scoloplos armiger*, the surface feeding detrivorous polychaetes *Levinsenia gracilis*, *Chaetozone* spp. and *Myriochele oculata* and the surface feeding detrivorous cumacean *Eudorella emarginata*. In the middle part of the fjord the fauna was specifically dominated by the, respectively, surface and subsurface feeding detrivorous polychaetes *Aricidea* spp. and *Praxillella affinis* and the subsurface feeding detrivorous bivalve *Thyasira minuta*. In the more shelf-water influenced outer margin of the fjord a specific dominance of the surface feeding detrivorous polychaete *Pseudopolydora paucibranchiata*, the suspensivorous polychaete *Jasmineira candela*, the suspensivorous epifaunal bivalve *Kelliella miliaris* and an unidentified species of the genus *Thyasira* were recorded. The proportion of deep subsurface head-down feeding polychaetes (*Heteromastus filiformis* and the Maldanidae) ranged between 12 and 56 % of the total abundance per station. It is suggested that such polychaete taxa, by depositing of faeces on the uppermost sediment layer and also by feeding selectively on relatively organic-rich particles, may have an important energy-exploiting role in communities occupying fine-particulated fjord sediments with relatively low concentrations of organic carbon.

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KEYWORDS: Northern Norway; soft bottom; macrofauna; glacier influence.

INTRODUCTION

Most European fjords are potentially affected by more or less local anthropogenic activities. Published results from quantitative investigations on soft-bottom macrofaunal communities which are evidently not exposed to pollution from local point sources are therefore difficult to find. Thus, benthic fjord surveys are often based on anthropogenic-induced motives and/or the results may be biased as a result of anthropogenic-derived environmental change. Quantitative unbiased faunal data from European fjords are needed both to achieve comparative results relative to pollution-induced changes and to study naturally occurring ecological interactions in fjord sediments. The aim of this paper is to document how soft-bottom macrobenthic communities, their populations and functional roles, may appear throughout an unpolluted northern European fjord. Hopefully, the results will be of value with regard to pollution-induced investigations where reference data from pristine areas are often needed and where the acquisition of such data is unfortunately not given priority. The study was demanded by the Norwegian State Pollution Authority (SFT) prior to a presumed future change of the fjord environment due to the building of a planned hydroelectric power plant including serious water-fall regulations.

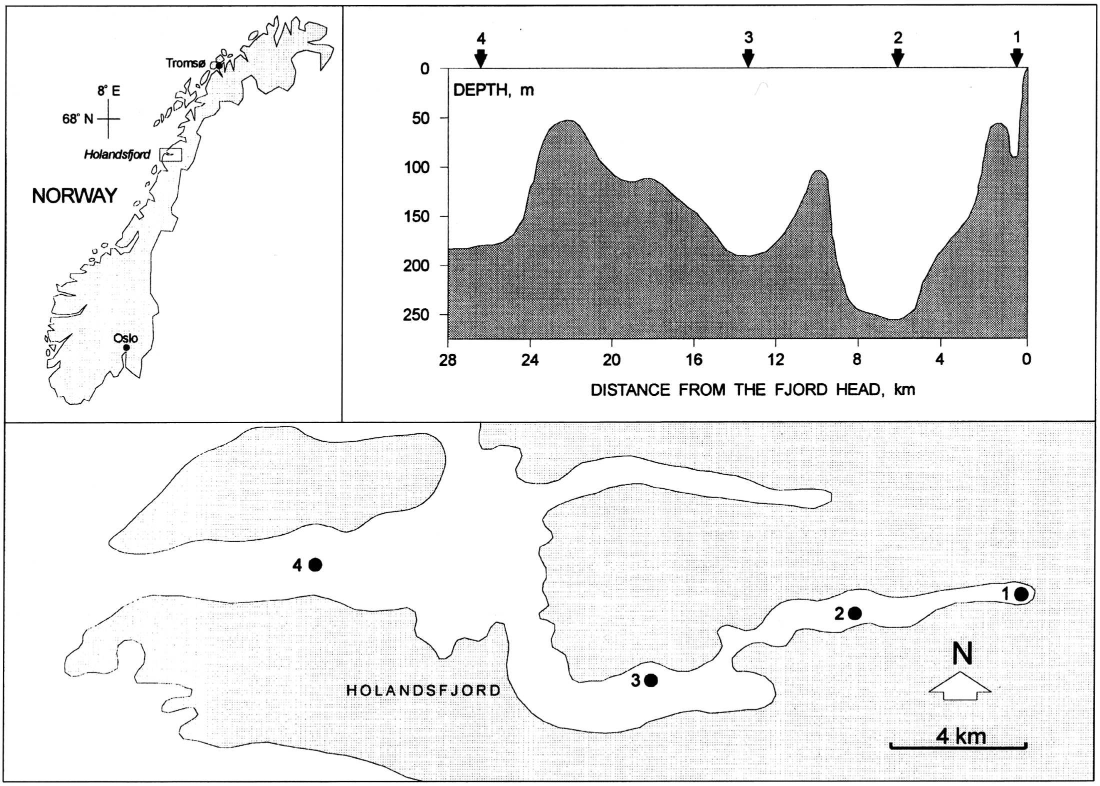

Fig. 1. Location of sampling stations and depth profile of the Holandsfjord (after Molvær & al. 1994).

STUDY AREA

The 30 km long Holandsfjord, located in Nordland county, Norway, has one minor inner basin with a maximum sill depth of ca 60 m and a maximum basin depth of 90 m and two major basins with maximum depths of 195 m and 240 m and maximum sill depths of 50 m and 100 m, respectively (Fig. 1). The Holandsfjord receives turbid melt-water from the ca 250 km^2 Svartisen glacier.

In order to describe the oceanographic conditions in the Holandsfjord before starting water-fall regulations, monthly surveys were carried out by Molvær & al. (1994) in the period May 1991 - December 1992. The lowest dissolved oxygen concentration in the bottom waters of the Holandsfjord was recorded as 6.2 mg l^{-1} (68 % saturation). The surface water (0-3 m) had salinities between 4-33 psu and temperatures between 3-18 °C, while 28-35 psu and 3.5-14 °C were recorded below the surface water. The water masses below the sill depths are probably exchanged annually by seasonal inflows of oceanic water with relatively high salinity (J. Molvær pers. commn). The two innermost basins of the fjord are usually ice-covered in December-April. The annual sedimentation rate was 4.6-8.4 kg m^{-2} at a depth of 70 m at the fjord head (20 m above the sea floor at the present Stn 1, see below), and 1.0 kg m^{-2} at 220 m depth about 7 km further out in the fjord (20 m above the sea floor at the present Stn 2, see below). These results correspond to accumulation rates of 8-16 mm and 2 mm yr^{-1}, respectively. The annual organic carbon flux to the bottom was calculated to between 78-116 g m^{-2} at the fjord head and between 35-39 g m^{-2} 7 km further out. Molvær & al. (1994) concluded that the innermost part of the Holandsfjord was impacted by glacier-derived inorganic sedimentation but that the fjord was undisturbed by anthropogenic activities.

MATERIAL AND METHODS

Four sampling stations were established with varying distance from the fjord head (Fig. 1). Sampling was carried out on 15-16 May 1991, 23-24 April 1992 and 14 October 1994. The last sampling took place after some major discharges of glacier melt-water just after the start-up of the power plant in late spring 1994. All four stations were sampled in 1991 and 1992, while Stns 3 and 4 were excluded in 1994 due to bad weather.

Four replicate samples were taken at each station using an 'off-shore' modified (reinforced) 0.1 m^2 van Veen grab with an inner volume of ca 18 l. The upper surface of each bucket of the grab was equipped with hinged inspection openings covered with outer flexible rubber flaps and a 0.5 mm mesh. To avoid resuspension of sediment while settling the grab, its lowering speed was decreased to ca 0.2 m s^{-1} just before it reached the sea floor. The samples were sieved through a 1 mm round-holed screen while submerged in water and then conserved in buffered formaldehyde with Rose Bengal dye. The four fauna samples taken at each station were unfortunately lumped, thus faunal variation between replicate samples could not be analysed.

Sub-samples for analyses of sedimental parameters were taken within the grab through the inspection openings. Grain-size samples were taken using a 5 cm diameter cylinder pushed 5 cm vertically into the sediments. Particles ≤ 0.063 mm were separated from coarser sediment fractions by wet-sieving and, after dispersion in an ultrasonic bath, analysed by X-ray particle counting using a Sedigraph 5100. Particles ≤ 0.063 mm and > 0.002 mm were denoted as silt while particles ≤ 0.002 mm were denoted as clay. Total organic carbon (TOC) and total nitrogen (TN) samples were taken from the surface sediment layer (0-2 cm) and analysed using a Carlo Erba CHN-analyser after removal of inorganic carbonates by acidification. One mixed sample, composed of one spoon-full of sediments (ca 10 ml) from each of the four replicate grab samples, was analysed pr. station.

Faunal diversity was calculated using the Shannon-Wiener index H (log-base 2) and the Hurlbert rarefaction function (Hurlbert 1971). The latter function, presented as curves, calculates the expected number of sampled taxa given a specific number of sampled individuals (here: 10, 20, 30, 40, 50, 100, 200, 300 … 1000 individuals).

Multivariate classification and ordination analyses were carried out using the software package 'NTSYS-pc Numerical Taxonomy and Multivariate Analysis System' developed by Rohlf (1989). The analyses were based on Bray-Curtis coefficient calculated from double square root transformed data. The classification analysis included group average sorting and goodness of fit calculations (correlation coefficient 'r'). The ordination analysis was carried out using Multidimensional Scaling (MDS) optimised by Principal Co-ordinate and Principal Component analyses, inclusive of a goodness of fit calculation, presented as 'Stress factor' (see Rohlf 1989).

The Spearman rank correlation coefficient was calculated for species abundance vs distance from the fjord head. The coefficient ranges from –1 to 1, where –1 is given for a taxon with a progressively decreasing abundance with increasing distance from the fjord head while 1 represents a taxon with progressively increasing abundance with distance. The calculations were based on the abundance for each taxon and for each of the three sampling years. Thus 10 data units (sampling stations) were included in each calculation (see Appendix).

RESULTS

Sediments

The sampled sediment volumes ranged at all the stations between 16-18 litres per replicate grab sample. The generally clay and silt dominated sediments (Table 1) varied in colour from dark grey to light grey without any smell of H_2S, indicating generally aerobic conditions through the sampled sediment column of 18 cm.

In all the three sampling years, respectively, the organic carbon content was 9, 10 and 14 mg g^{-1} at Stn 1, 11 mg g^{-1} at Stn 2, 7 mg g^{-1} at both sampling years at Stn 3, and 21 and 22 mg g^{-1} at Stn 4 (Fig. 2). However, and as pointed out by Rygg (1995) who presented TOC and sediment grain size relations from Norwegian coastal areas, it is important to bear in mind that the organic carbon content in sediments is mainly associated with the silt-clay fraction (< 0.063 mm). Compared to Rygg's (1995) data from sites with similar clay-silt content as the stations in the Holandsfjord, the TOC content at Stns 4-91 and 4-92 was relatively high while the TOC content at Stns 1-94, 2-92, 2-94, 3-91 and 3-92 was relatively low (Fig. 2). The nitrogen content ranged from 1.0 to 1.3 mg g^{-1} at Stns 1, 2 and 3 and from 3.0 to 3.2 mg g^{-1} at Stn 4. The carbon-nitrogen ratio ranged from 7 to 12 with the lowest values at the outermost part of the fjord (Stns 3 and 4). The carbon-nitrogen ratio at Stns 3-92 and 1-94 may be under-estimated due to nitrogen concentrations that were lower than the detection limit of 1 mg g^{-1} which were used to calculate the ratio at these two stations.

Fauna

A total of 10 506 individuals and 109 taxa, representing 8 phyla, were recorded (see Appendix for complete fauna list and abundance data). The Annelida was the

Table 1. Depth, total abundance, number of taxa, clay+silt content and total organic carbon (TOC) concentrations at each station and sampling year.

Stn	Depth	No. of individuals m^{-2}			No. of taxa			Clay + Silt, %			TOC, mg g^{-1}		
	m	-91	-92	-94	-91	-92	-94	-91	-92	-94	-91	-92	-94
1	95	3942	4680	4910	40	34	45	4+26	9+53	33+54	10	14	9
2	240	3650	2625	1628	39	31	34	17+45	22+73	58+37	11	11	11
3	195	970	3048	-	23	34	-	11+73	16+78	-	7	7	-
4	180	480	373	-	30	38	-	5+57	13+67	-	21	22	-

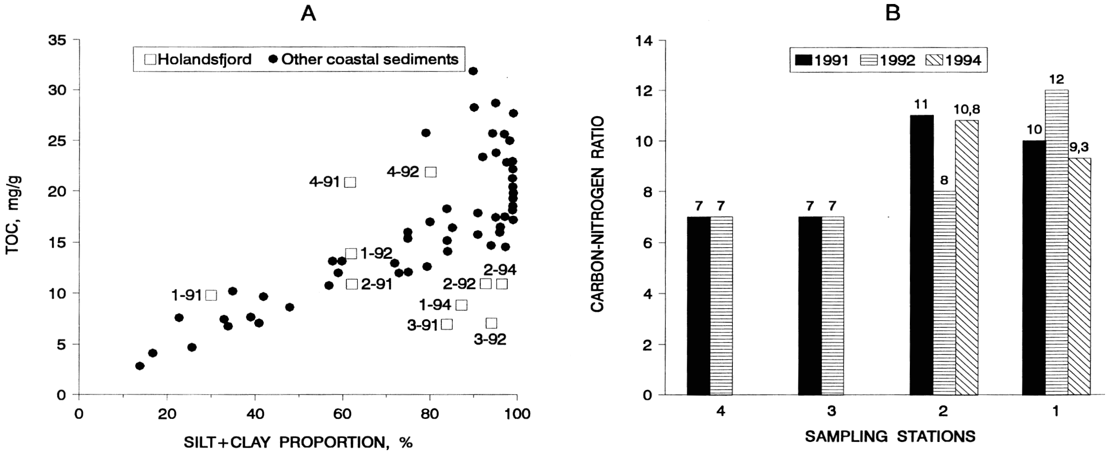

Fig. 2. Organic carbon content (dry weight) in the sediments relative to the proportion of clay and silt (A) and carbon/nitrogen ratio (B) for each sampling station and sampling year in the Holandsfjord. The organic carbon content in the surface sediment at 67 stations in other Norwegian fjords and coastal waters is shown (A) (data from Rygg 1995).

most numerous phylum, both relative to number of specimens (9152) and taxa (58). The second most numerous phylum was the Mollusca with 25 taxa, of which 21 were bivalves. The third most frequently occurring phylum was the Crustacea with 20 taxa. The most numerous species in the Holandsfjord was the paraonid polychaete *Levinsenia gracilis* with a total of 1884 sampled individuals (see Table 2 for mean abundance), which represent 18 % of the total number of individuals recorded, followed by the capitellid polychaete

Table 2. The ten most abundant taxa at each station and sampling year (presented as mean abundance m^{-2} yr^{-1}), functional roles (shown by indented taxa names) and Spearman rank coefficient calculated with regard to abundance vs distance from the fjord head (presented as mean value yr^{-1}). The taxa are listed in descending abundance. B = Bivalves; C = Crustaceans; P = Polychaetes.

Taxon	Station				Spearman rank
Detrivores Suspensivores Carnivores	1	2	3	4	
Levinsenia gracilis (P)	1471	5	135	6	– 0.61
Heteromastus filiformis (P)	659	546	139	65	– 0.81
Myriochele oculata (P)	589	133	151	6	– 0.74
Chaetozone spp. (P)	318	4	41	4	– 0.64
Maldane sarsi (P)	318	530	324	3	– 0.40
Prionospio cirrifera (P)	221	26	256	23	– 0.44
Scoloplos armiger (P)	163		56		– 0.68
Ceratocephale loveni (P)	154	215	29	1	– 0.63
Lumbrineris sp. (P)	117	394	194	9	– 0.33
Eudorella emarginata (C)	65	6			– 0.95
Yoldiella lenticula (B)	48			51	– 0.04
Aricidea spp. (P)	4	43	50	1	0.01
Pseudopolydora paucibranchiata (P)	3			11	0.35
Thyasira minuta (B)		288	279	5	– 0.39
Terebellides stroemi (P)		106	53	59	0.57
Praxillella affinis (P)		68	29		0.04
Yoldiella lucida (B)		43	63	36	0.65
Yoldiella nana (B)		18	118	25	0.72
Thyasira sp. (B)		2	1	10	0.55
Jasmineira candela (P)				14	0.48
Kelliella miliaris (B)				11	0.71

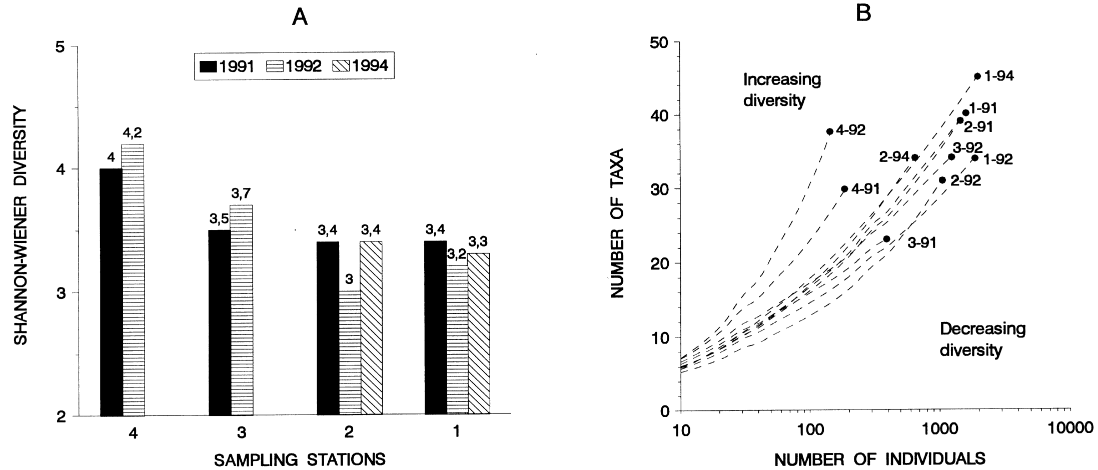

Fig. 3. The Shannon-Wiener diversity (A) and the Hurlbert rarefaction function (B) for each sampling station and sampling year.

Heteromastus filiformis (1609 individuals; 15 %) and the maldanid polychaete *Maldane sarsi* (1278 individuals; 12 %).

The number of recorded taxa per station ranged from 23 to 45 while the total abundance varied from 373 to 4910 ind. m^{-2} (Table 1). The highest number of individuals was in all sampling years recorded at Stn 1, where also the highest number of taxa was found in 1991 and 1994. The lowest number of individuals was recorded at Stn 4 and the lowest number of taxa at Stns 2 (1992) and 3 (1991). The Shannon-Wiener diversity index varied between 3.0 (Stn 2-92) and 4.2 (Stn 4-92) (Fig. 3). Although no clear trends appeared with regard to distance from the fjord head, the Hurlbert rarefaction curves showed relatively high diversity at Stn 4 compared to the other stations (Fig. 3).

Among the ten most abundant taxa per station ('top-ten' taxa, Table 2), the species that were clearly most frequent specifically at Stn 1 (see Appendix) were the surface feeding detrivorous polychaetes *Levinsenia gracilis*, *Chaetozone* spp. and *Myriochele oculata*, the subsurface feeding detrivorous polychaete *Scoloplos armiger*, and the surface feeding detrivorous cumacean *Eudorella emarginata.* In addition to the quite abundant carnivorous polychaetes *Ceratocephale loveni* and *Lumbrineris* sp., the most abundant and widespread taxa throughout the Holandsfjord seemed to be the deep subsurface feeding detrivorous polychaetes *Heteromastus filiformis* and *Maldane sarsi.* Three species specifically occurred with relatively high abundances at Stns 2 and 3, namely the subsurface feeding detrivorous bivalve *Thyasira minuta*, the deep subsurface feeding maldanid polychaete *Praxillella affinis* and the presumed surface feeding detrivorous genus *Aricidea* spp. Five taxa, the suspensivorous bivalve *Kelliella miliaris*, the suspensivorous polychaete *Jasmineira candela*, the surface feeding detrivorous spionid polychaete *Pseudopolydora paucibranchiata* and the subsurface feeding detrivorous bivalves *Thyasira equalis* (see Appendix) and *Thyasira* sp., almost solely occurred at Stn 4. Apart from one individual of *Terebellides stroemi* at Stn 1-91, this surface feeding detrivorous polychaete and the two subsurface feeding detrivorous bivalves *Yoldiella lucida* and *Yoldiella nana* were not recorded at Stn 1 while they were relatively frequent at the other stations.

Eudorella emarginata showed the most negative Spearman rank correlation (correlation coefficient = –0.95; Table 2), followed by *Heteromastus filiformis* (–0.81) and *Myriochele oculata* (–0.74), while the three most positively correlated taxa were *Kelliella miliaris* (0.71), *Yoldiella nana* (0.72) and *Yoldiella lucida* (0.65).

The cluster analysis separated Stn 4 from all the other stations at a similarity level of 34-45 %. At the similarity level of 45-50 % three separate clusters of stations were identified (Fig. 4) where one consists of Stn 1 (1-91, 1-92, 1-94), one of the Stns 2 and 3 (2-91, 2-92, 2-94, 3-91, 3-92) while the third cluster consists of Stn 4 (4-91, 4-92). The ordination analysis seemed to confirm the classification analysis as Stns 1 and 4 were clearly separated while Stns 2 and 3 occupied an intermediate position (Fig. 4). Compared to the classification analysis the ordination analysis seemed to separate more clearly Stns 2 and 3. Both the classification and the ordination analyses showed a good fit to the Bray-Curtis matrix with a correlation coefficient (r) of 0.86 ('good fit'; ROHLF 1989) and a final stress factor of 0.15 ('fair' to 'good' fit; ROHLF 1989).

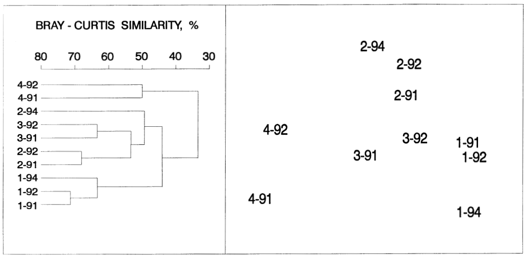

Fig. 4. Classification (left) and MDS ordination plots (right).

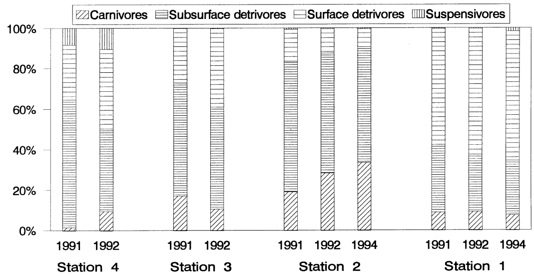

Fig. 5. Accumulated proportion of sampled Annelida and Mollusca individuals separated into functional roles at each sampling station and sampling year (function per taxon is shown in the Appendix).

DISCUSSION

Based on the data from Molvær & al. (1994), and also the results and discussion presented by Farrow & al. (1983) who investigated the glacial fjord Knight Inlet, British Columbia, the sediment regime at the head of the Holandsfjord (Stn 1) is most likely exposed to relatively high sedimentation rates of organic carbon, while the carbon concentration in the sediments is nevertheless relatively low due to elevated inorganic sedimentation. This situation is probably linked to glacier influence and the high total sedimentation rates (8-16 mm year^{-1}; Molvær & al. 1994) compared to non-glacial Norwegian fjords where sedimentation rates of around 1 mm year^{-1} are known to occur (Skei & Paus 1979; Wassmann 1983; Skei & al. 1986; Syvitski & al. 1987; Næs 1991). The sediment regime further out than Stn 2 was not surveyed by Molvær & al. (1994) but it is, however, suggested that the generally relatively low organic carbon concentration at the sampling stations within all the three basins of the Holandsfjord is a result of glacial influence. Similar carbon concentrations have been recorded in silt–clay dominated sediments in Arctic glacial fjords (Görlich & al. 1987; Feder & Jewett 1988) as well as in sediments that are polluted by inorganic and inert fine-particulated mine-tailings in the Norwegian fjords Bøkfjord, Ranafjord and Jøssingfjord (Skei & Rygg 1989; Olsgard & Hasle 1993; Helland & al. 1994; Skei & al. 1995). Moreover, Syvitski & al. (1987) claimed that the benthos in deep and high-latitude fjords, especially in glacial fjords, is typically carbon limited. Although some terrestrial carbon input may occur at the two innermost stations in the Holandsfjord, the food supply to the sediments probably is mainly of natural marine origin (plankton) as indicated by the carbon-nitrogen ratios ranging between 7.0 and 12.0 (see Prahl & al. 1994).

Even though the number of stations may be too low to achieve a continuous along-fjord understanding of the faunal assemblages in the Holandsfjord, the Shannon-Wiener diversity index and the Hurlbert diversity curves indicate that the diversity was lower in the main part of the fjord (Stns 1, 2 and 3) than at the outermost sampling station (Stn 4). For each specific sampling year the taxa with the most apparent numerical change throughout the fjord were the polychaetes *Levinsenia gracilis*, *Prionospio cirrifera*, *Chaetozone* spp. and *Myriochele oculata* (see Appendix). Apart from possible ecological interactions, which are discussed below, the faunal differences between the inner- and outermost part of the Holandsfjord, which e.g. were demonstrated through the classification and ordination analyses, are believed to reflect the difference in depth, composition of suspended material in the bottom water, and the organic carbon content in the sediments. Considering the most common species in the Holandsfjord (Table 2), the suspensivores were represented by the sabellid tubicolous polychaete *Jasmineira candela* and the bivalve *Kelliella miliaris*, both only recorded at the outermost sampling station (Stn 4) which is probably more influenced by shelf waters than the other stations (Fig. 5). Their distribution patterns may indicate that the sedimentation regime in the main part of the Holandsfjord is disadvantageous to some suspensivorous taxa (see Moore 1977; Hyland & al. 1994). In their larval and juvenile stages other species with other feeding habits may also be vulnerable to excess fine-particulated sedimentation. Thus the bivalves, which largely comprised subsurface detrivores, were clearly less frequent at the innermost sampling station (the fjord head, Stn 1) than at the other stations. Nevertheless, the absence of molluscs at Stn 1-92 was surprising and is probably related to the nature of the physical environment in the innermost part of the Holandsfjord. This may be a result of high sedimentation rates with a relatively high inorganic fraction and possibly also patchy distribution of the molluscs.

The proportion of detrivores was highest at Stn 1 (91 % in all sampling years), Stn 3-92 (89 %) and Stn 4-91 (90 %) (Fig. 5). Due to the very low abundance of suspensivores at Stns 1, 2 and 3, the proportion of detrivores at these stations varied solely with the proportion of carnivores, reflecting the apparently more diverse community at Stn 4. A difference in faunal composition between the main body of the Holandsfjord and its outer margin is, however, not surprising as these two regions represent quite different environments, namely one typical sill basin environment with supposed relatively low bottom current velocities, low horizontal water exchange and high sedimentation rates, and another one with a more or less shelf-influenced environment with relatively low sedimentation rates and high horizontal water exchange. The distribution of carnivores was assumed to be prey-dependent (JOSEFSON 1987; LEVIN & al. 1991) and was therefore not given any further attention. It was, however, noticed that the polychaetes *Ceratocephale loveni* and *Lumbrineris* sp. were very abundant at Stn 2 (Table 2; see Fig. 5), which might explain the relatively low abundance for some possible prey species at this station such as *Scoloplos armiger*, *Chaetozone* spp., *Prionospio cirrifera* and *Levinsenia gracilis*. Lumbrinerid polychaetes are common in silty sediments along the coast of Norway and in the western Spitsbergen fjords, while the nereid *Ceratocephale loveni* has not been recorded at Svalbard and has – in contrast to the present results – been recorded in relatively low densities in northern Norwegian waters (< 40 ind. m^{-2}, see e.g. RYGG 1983, KIRKERUD & al. 1985, BERGE & al. 1993, LARSEN & al. 1993, BERGE & al. 1994, HOLTE & OUG 1996).

Possible species-dependent depth-preferences between Stn 1 (95 m) and the other sampling stations (195-240 m) may have influenced the along-fjord faunal differences recorded in the Holandsfjord. In order to identify any such decisive faunal depth preferences, and also in order to identify any otherwise environmental-dependent species-related abundances, autecological data for the most frequent taxa at Stn 1, and taxa which in addition showed clearly negative correlations to distance from the fjord head, were reviewed with respect to their occurrence in northern Norwegian and adjacent coastal waters (mainly Norway and Svalbard). Depth-dependence for the respective taxa was interpreted relative to the results in the reviewed publications and reports from these areas, which is not necessarily in accordance with depth-tolerances generally known from other published literature.

Eudorella emarginata (Crustacea, Cumacea)
In contrast to the present findings and also those made by SKEI & RYGG (1989) in the inorganic mine-tailings polluted Bøkfjord, *E. emarginata* showed decreasing abundance in the Jøssingfjord with respect to increasing inorganic impacts (OLSGARD & HASLE 1993). On the other hand, RYGG (1985) found that *E. emarginata* does not thrive in organic enriched environments. The species is not very common in northern Norwegian coastal waters. *E. emarginata* has, however, been recorded in relatively high densities (55 individuals m^{-2}) at depths between 26 and 50 m in the inner part of the Ofotfjord (LARSEN & al. 1993). Thus, its occurrence in the Holandsfjord might have been influenced by depth-dependent factors. Autecological and detailed functional data on *E. emarginata* are scarce.

Heteromastus filiformis (Polychaeta, Capitellidae)
H. filiformis is known as a highly opportunistic (e.g. PEARSON & ROSENBERG 1978) species relative to organic enrichment and is tolerant to hypoxic and temporary anoxic sediments (OESCHGER & VISMANN 1994). It probably feeds selectively on the clay-silt fraction in a head-down position down to 20 cm below the sediment surface (CADEE 1979; NEIRA & HÖPNER 1994). At 300 m depth at assumed pristine sites in Northern Norway, *H. filiformis* has been recorded in densities of up to 800 individuals m^{-2} (LARSEN & al. 1993) while more than 4000 individuals m^{-2} were recorded at depths of 6-8 m close to Tromsø (HOLTE & GULLIKSEN 1987). OLSGARD & HASLE (1993) found *H. filiformis* greatly dominating the fauna in mine-tailings influenced sediments characterised by relatively low organic content. Its occurrence in the Holandsfjord is thus probably not depth-dependent.

Myriochele oculata (Polychaeta, Oweniidae)
Whether *M. oculata* is a surface or a subsurface feeder may be a matter of discussion and there are obviously different opinions among benthic scientists. However, BAMBER'S (1984) laboratory observations of feeding specimens living in natural mud are convincing. He claims that *M. oculata* (sampled from the North Sea) is a deposit feeder which selectively grazes surface particles.

The great quantitative difference for *M. oculata* between the two innermost stations in the Holandsfjord may indicate a depth-dependent distribution, which was also found in the Ofotfjord by LARSEN & al. (1993). However, results from the Ranafjord (HELLAND & al. 1994) indicated an extended depth tolerance for *M. oculata* compared to the present observations in the Holandsfjord. Nevertheless, the four-fold density at Stn 1 compared to Stn 2 suggests a substantial tolerance to organic-poor sediments. In contrast, the species has also been recorded at relatively high densities in stagnant organic polluted and periodically oxygen-depleted northern Norwegian coastal waters (OUG & HOLTE 1985). Thus, *M. oculata* seems to occur in relatively high abundances in quite different environments.

Scoloplos armiger (Polychaeta, Orbiniidae)
Through its abundance, *S. armiger* was found to clearly dominate the innermost parts of the glacier-influenced Spitsbergen fjords Hornsund and Isfjord (Weslawski & al. 1990; Gromisz 1992; Kendall & Aschan 1993) and is known as a moderately opportunistic taxon relative to organic enrichment (Pearson & Rosenberg 1978; Gray & al. 1990; Holte & Oug 1996). In northern Norwegian coastal waters *S. armiger* has been recorded in varying densities in both pristine and anthropogenically influenced areas, which was also indicated by Pearson & Rosenberg (1978). In the organic enriched areas in the Oslofjord, Glomfjord and the Surnadalsfjord, *S. armiger* was rare (Næs & al. 1982; Aschan & Skullerud 1990; Rygg 1992), while densities of up to 500 individuals m^{-2} were recorded in the slightly carbon-enriched shallow areas around Tromsø (Holte & Gulliksen 1987; Holte & Oug 1996). At shallow sites (30 m depth) in the Narvik harbour, a density of 150 individuals m^{-2} was observed while 325 individuals m^{-2} were recorded at similar depths in other relatively undisturbed areas in the inner part of the Ofotfjord (Larsen & al. 1993). At five other sites between 150 and 350 m depth, *S. armiger* was scarce (< 6 ind. m^{-2}). In contrast to the relatively high densities in the Holandsfjord, this species was not numerically dominant in the inorganic impacted Jøssingfjord and did not show a mine-tailings controlled distribution in the Bøkfjord (Skei & Rygg 1989; Olsgard & Hasle 1993). These records indicate that the occurrence of *S. armiger* may be unpredictable relative to specific environmental conditions. Its role as an 'indicator-species' towards specific environmental conditions might therefore be questioned in spite of its 'opportunistic-like' life history (Giangrande & Petraroli 1991). Based on findings from northern Norwegian fjords, its occurrence in the Holandsfjord may be depth-dependent (see Table 2). However, Hartmann-Schröder (1971) claims that this species occurs from the eulittoral to depths of 2000 m.

Chaetozone spp. / *C. setosa* (Polychaeta, Cirratulidae)
The taxon *Chaetozone* spp. is comprised of 70-80 % *C. setosa* Malmgren, 1867 and 20-30 % of the genus *Tharyx*. The cirratulid complex is confusing and the *Chaetozone* genera should be revised (Woodham & Chambers 1994). *C. setosa* might therefore often have been identified to *Chaetozone* sp./spp.. *Chaetozone* spp. seem generally to be the most stable taxon with respect to the frequency of occurrence in areas highly influenced by glacier-induced inorganic sedimentation at Svalbard (Gulliksen & al. 1985; Weslawski & al. 1990; Gromisz 1992; Kendall & Aschan 1993; Holte & al. 1996) but is, in contrast, also known to occur in relatively high densities in organic enriched sediments (Rygg 1985; Hily 1987; Holte & Gulliksen 1987; Holte & Oug 1996). Moore (1974) found the cirratulids to be particularly prevalent in turbid areas, while Aschan & Skullerud (1990) observed *Chaetozone* in relatively high abundance in organic polluted areas in the Oslofjord. As was recorded in the Holandsfjord, the highest abundance of the genus *Chaetozone* was found in the innermost parts of the glacier-influenced Svalbard fjords Hornsund (Gromisz 1992) and Raudfjord (Gulliksen & al. 1985). This taxon should therefore be regarded as tolerant to physical disturbance, which was also noted by Feder & Jewett (1988). *Chaetozone* does not show specific depth preferences in Norwegian or Svalbard coastal waters.

Levinsenia gracilis (Polychaeta, Paraonidae)
In contrast to the present observations in the Holandsfjord, the abundance of *L. gracilis* has not been found to exceed 70 individuals m^{-2} at undisturbed sites in Northern Norway (20 to 500 m depth; Berge & al. 1993; Larsen & al. 1993; E. Oug pers. commn). In the Glomfjord, *L. gracilis* occurred at only one out of several sampled stations and with an abundance of eight individuals m^{-2} (200 m depth) (Næs & al. 1982). The organic content in the sediment surface at this single station was approximately 60 mg g^{-1} TOM (total organic material). In the organic enriched recipient waters close to Oslo and Tromsø, *L. gracilis* was recorded at densities of 2-4 ind. m^{-2} (Aschan & Skullerud 1990; Holte & Oug 1996). Thus, the abiotic conditions in the inner part of the Holandsfjord and/or the specific ecological condition this physical environment may give rise to, seem suitable for *L. gracilis*. This was also interpreted from the data presented by Skei & Rygg (1989) from the most inorganic affected sites at 90 and 110 m depth in the Bøkfjord (207 ind. m^{-2}). In contrast, the species showed no obvious tolerance to the most inorganic affected sites at similar depths in the Jøssingfjord (Olsgard & Hasle 1993). In the glacier-influenced Isfjord system at Svalbard, Holte & al. (1996), who surveyed depths between 20 and 150 m, recorded only two individuals m^{-2}. Kendall & Aschan (1993) found up to 400 individuals m^{-2} in the Oslofjord (30-35 m depth) while *L. gracilis* was not recorded by Weslawski & al. (1990) in the Isfjord, Svalbard (10-70 m).

Prionospio cirrifera (Polychaeta, Spionidae)
P. cirrifera has been recorded along the whole Norwegian coastline in both relatively undisturbed (e.g. Rygg 1992; Helland & al. 1994) and in organically enriched areas (e.g. Aschan & Skullerud 1990; Holte & Oug 1996). In contrast to the present results, this species has been scarcely represented in mine-tailings affected

sediments (Skei & Rygg 1989; Olsgard & Hasle 1993). In Northern Norway, *P. cirrifera* seems to occur in clay-silt dominated sediments from shallow sublittoral waters to depths of ca 500 m and its maximum abundance varies profoundly within this depth interval (Kirkerud & al. 1985; Helland & Rygg 1990; Helland & Rygg 1991; Berge & al. 1993; Larsen & al. 1993). Its highest density in Northern Norway was recorded by Helland & al. (1994) as 1650 ind. m^{-2} at 100 m depth in the Ranafjord. Its occurrence in the Holandsfjord was relatively high at the stations 1 and 3, and low at Stn 2 (Table 2), thus as well indicating an independent frequency of occurrence with regard to major depth differences.

Maldane sarsi (Polychaeta, Maldanidae)
M. sarsi is an up to 10 cm long, head-down feeding detrivore (Fauchald & Jumars 1979) that disposes faecal pellets on the sediment surface. It has been recorded at depths from 8 to 4400 m (Hartmann-Schröder 1971). In the Holandsfjord, it was the second most abundant species at Stn 2 and the fourth most abundant at Stn 1. Although little data about *M. sarsi* are published, it is well-known at various depths along the coast of Norway and Svalbard.

With the possible exception of *Eudorella emarginata*, the abundances of the above reviewed taxa are probably not primarily depth dependent in the Holandsfjord. The least frequent of them in northern Norwegian waters seems in general to be *Eudorella emarginata* and *Levinsenia gracilis*. The very high abundance of *L. gracilis* in the Holandsfjord was therefore unexpected. However, this species is, as most paraonid polychaetes, very small with an adult wet biomass of ca 0.2-0.5 mg per individual (author's estimate). A biomass of up to 1 g m^{-2} for this species might thus be present at e.g. Stn 1 in 1994 (1875 individuals m^{-2}), indicating that a relatively abundant population may arise in relatively carbon-poor sediments. Regarding its low frequency of occurrence in Norwegian coastal waters in general, the high abundance of *Levinsenia gracilis* at the head of the Holandsfjord may more or less define its environmental and ecological preferences in northern coastal waters.

According to the results in Clough & Lopez (1993) and Neira & Höpner (1994) *Heteromastus filiformis* transports significant amounts of organic carbon through its gut system from deep sediment layers where it feeds, to the sediment surface where its faecal products are deposited. Additionally, Neira & Höpner (1994) found that *H. filiformis* produced faecal pellets with a higher organic content than the sediments it was feeding in (55 % clay-silt), indicating that *Heteromastus filiformis* feeds selectively with respect to both organic matter and to sediment grain size (< 0.063 mm) (despite the fact that these two physical parameters generally are strongly associated to each other). Although spectacular exceptions may occur (McDaniel & Banse 1979), the maldanid polychaetes have a similar functional role and physical position in the sediments as the capitellid polychaete *Heteromastus filiformis* (Mangum 1964; Day 1967; Fauchald & Jumars 1979). It is therefore suggested that the recorded maldanids in the Holandsfjord (*Nicomache*, *Rhodine*, *Praxillella* (two species), *Asychis*, *Maldane*; see Appendix), in terms of energy and for the benefit of the whole community, together with *H. filiformis* contribute to a 'cost-effective' transfer of organic carbon from deep sediment layers to the surface top-slice. After mineralisation and/or physical destruction by meiofauna or micro-organisms (see e.g. Neira & Höpner 1994), the energy in the faecal products are probably available for most surface associated deposit feeders (e.g. the present recorded *Chaetozone* spp., *Prionospio cirrifera*, *Myriochele oculata*, *Terebellides stroemi*, *Eudorella emarginata*). Thus, it is suggested that the head-down deep subsurface feeding detrivorous polychaetes may have a relatively important energy-exploiting role in communities occupying relatively carbon-poor fine-particulated sediments. Such a functional role might in particular have taken place at the present Stn 2 where the deep subsurface feeding polychaetes comprised between 36-58 % of the total number of individuals in the respective sampling years, while less than 26 % occurred at the other sampling stations.

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Appendix. Total fauna list for each sampling station and sampling year (1991, 1992. 1994) in the Holandsfjord. Functional roles for the Annelida and the Mollusca are shown: 'carn' = carnivore; 's.detr' = surface feeding detrivore; 'ss.detr' = subsurface feeding detrivore; 'susp' = suspensivore.

Taxa		No. of individuals per sampling station (0.4 m^2)									
		1-91	1-92	1-94	2-91	2-92	2-94	3-91	3-92	4-91	4-92
PROTOZOA											
Foraminifera sp.				1	1						
CNIDARIA											
Edwardsia sp.		3			2	2		3			
NEMERTINI											
Nemertini indet.		6	9	5	8	16	3	1	2		1
SIPUNCULIDA											
Golfingia sp.				13	19	7					
ANNELIDA											
Polychaeta											
Paramphinome jeffreysii (McIntosh,1868)	carn	3	19	17			1				
Antinoella sarsi (Malmgren, 1865)	carn	2	2	13	3	2	17				1
Pholoe inornata Johnston, 1839	carn			1							
Pholoe synopthalmica Claparède, 1868	carn			5		1					
Eteone flava (Fabricius, 1780)	carn	6									
Hesionidae indet.			1								
Exogone verugera (Claparède, 1868)	s.detr		1	1		1		3	10	1	
Ceratocephale loveni Malmgren, 1867	carn	36	78	71	80	95	83	8	15		1
Nereis sp.	carn					1					
Glycera alba (O.F. Müller, 1776)	carn	1	1	9							
Nephtys ciliata (O.F. Müller, 1776)	carn	14	16	3	5	4	3	6	6		6
Nephtys paradoxa Malm, 1874	carn		3						1		
Lumbrineris sp.	carn	73	50	17	185	183	105	50	105	2	5
Orbinia norvegica (M. Sars, 1872)	ss.detr										2
Scoloplos armiger (O.F. Müller, 1776)	ss.detr	93	65	38		1			45		
Aricidea sp. 1	s.detr	2	3		22	30		26	14		1
Aricidea sp. 2	s.detr	2									
Aricidea sp. 3	s.detr		1						2	1	
Levinsenia gracilis (Tauber, 1879)	s.detr	384	631	750	4	1	1	36	72	5	
Cossura sp.	ss.detr	4	26	1	2	1		2	8		
Laonice cirrata (M. Sars, 1851)	s.detr	7	1								
Prionospio cirrifera (Wirén, 1883)	s.detr	61	129	75	17	4	10	26	179	14	4
Polydora sp.	s.detr		1								
Pseudopolydora paucibranchiata (Okuda, 1937)	s.detr			3						1	8
Malacoceros fuliginosa (Claparède, 1869)	s.detr		1	3					2		
Spio sp.	s.detr	11	7	44			2				
Spiophanes kroeyeri Grube, 1860	s.detr	1	1		3	2	22		1		7
Chaetozone spp.	s.detr	138	120	123	4		1	6	27	3	
Capitomastus minimus (Langerhans,1880)	ss.detr				2						
Heteromastus filiformis (Claparède, 1864)	ss.detr	267	270	254	277	226	152	17	94	22	30
Nicomache lumbricalis (Fabricius, 1880)	ss.detr	1	4	1	1						
Rhodine gracilior Tauber, 1879	ss.detr										1
Praxillella affinis (M. Sars, 1872)	ss.detr				40	42			23		
Praxillella praetermissa (Malmgren,1865)	ss.detr				3	1	10		4		
Asychis biceps (M. Sars, 1861)	ss.detr				12	12	2				
Maldane sarsi Malmgren, 1865	ss.detr	78	143	160	204	306	126	85	174		2
Ophelina acuminata Oersted, 1893	ss.detr				1			1	4		1
Opheliidae indet.	ss.detr	6			8						
Polyphysia crassa (Oersted, 1843)	ss.detr	1			1						

Appendix (continued)

Taxa		No. of individuals per sampling station (0.4 m^2)									
		1-91	1-92	1-94	2-91	2-92	2-94	3-91	3-92	4-91	4-92
Scalibregma inflatum Rathke, 1843	ss.detr	1		2	1	4					
Myriochele oculata Zaks, 1922	s.detr	280	247	180	154	4	1	5	116	1	4
Diplocirrus glaucus (Malmgren, 1867)	s.detr		3	10	1						3
Chone sp.	susp		1						1		
Jasmineira candela (Grube, 1875)	susp										11
Euchone sp.	susp			2							1
Sabellidae indet.	susp	1								1	1
Pectinaria hyperborea (Malmgren, 1866)	ss.detr	17	12								
Pectinaria sp.	ss.detr			1							
Ampharete sp.	s.detr				1				2		1
Sabellides borealis M. Sars, 1856	s.detr			1							
Amythasides macroglossus Eliason, 1955	s.detr					1				1	1
Sosanopsis wireni Hessle, 1917	s.detr										1
Amage auricula Malmgren, 1866	s.detr										1
Melinna cristata (M. Sars, 1851)	s.detr										1
Laphania boecki Malmgren, 1866	s.detr	2							2		
Leaena ebranchiata (M. Sars, 1865)	s.detr	1			2		2				
Terebellidae indet.	s.detr				1					2	
Terebellides stroemi M. Sars, 1853	s.detr	1			29	80	18	2	40	21	26
CRUSTACEA											
Cumacea											
Eudorella emarginata (Kröyer, 1846)		14	11	53	1	1	5				
Leucon acutirostris G.O. Sars, 1864				1							
Campylaspis rubicunda Lilljeborg, 1855											1
Diastylis cornuta Boeck, 1863										1	
Diastylis scorpioides (Lepechin, 1778						1					
Diastylis sp.			7	3						1	
Tanaidacea											
Apseudes spinosus (M. Sars 1858)							1				
Amphipoda											
Neohela monstrosa (Boeck, 1861)							1				
Tmetonyx sp.							2				
Eriopisa elongata (Bruzelius, 1859)										3	
Arrhis phyllonyx (M. Sars, 1858)		4		9							
Monoculodes packardi Boeck, 1871		2	1	10				1	3		
Paroediceros propinquus (Goës, 1866)		1									
Harpinia antennaria Meinert, 1890							2				
Harpinia propinqua G.O. Sars, 1891					15	5					
Leptophoxus falcatus (G.O. Sars, 1882)							1			1	
Paraphoxus oculatus (G.O. Sars, 1879)					1						
Hyperiidae indet.							1				
Isopoda											
Eurycope sp.									1		
Decapoda											
Calocaris coronatus (Trybom, 1904)											1
MOLLUSCA											
Caudofoveata											
Chaetoderma sp.	carn	3		2				1			
Gastropoda											
Lacuna vincta (Montagu, 1803)	herb									1	1
Polinices pallidus (Broderip & Sowerby,1829)	carn			1				1		1	1
Philine sp.	carn								1		

Appendix (continued)

Taxa		No. of individuals per sampling station (0.4 m^2)									
		1-91	1-92	1-94	2-91	2-92	2-94	3-91	3-92	4-91	4-92
Bivalvia											
Nuculoma tenuis (Montagu, 1808)	ss.detr	21		10				2			
Nuculana pernula (Müller, 1779)	ss.detr									4	1
Yoldiella lenticula (Möller, 1842)	ss.detr	24		34						30	11
Yoldiella lucida (Lovén, 1846)	ss.detr				43		8	49	1	25	4
Yoldiella nana (M. Sars, 1865)	ss.detr				7		14	46	48	18	2
Yoldiella solidula Warén, 1989	ss.detr			2							
Mytilus edulis L., 1758	susp			1							
Delectopecten vitreus (Gmelin, 1791)	susp				1						
Pseudamussium septemradiatum (Müller, 1776)	susp									1	
Thyasira equalis (Verrill & Bush, 1898)	ss.detr								1	8	
Thyasira gouldi (Philippi, 1845)	ss.detr	4		2							
Thyasira minuta (Verrill & Bush, 1898)	ss.detr				302		44	13	210	3	1
Thyasira obsoleta (Verrill & Bush, 1898)	ss.detr									1	
Thyasira sarsii (Philippi, 1845)	ss.detr										1
Thyasira sp.	ss.detr					1	1	1		6	2
Astarte crenata (J.E. Gray, 1824)	susp				2	1					
Astarte sulcata (da Costa, 1778)	susp			5							
Cerastoderma edule (L., 1758)	susp			1							
Abra nitida (Müller, 1776)	susp	1		20	2	1	1			5	1
Kelliella miliaris (Philippi, 1844)	susp									8	1
Cuspidaria sp.	carn						2				
ECHINODERMATA											
Asteroidea											
Ctenodiscus crispatus (Retzius, 1805)		3	4	3	1				2		
Ophiuroidea											
Ophiura sarsii Lütken, 1858				1							
SUM		1577	1872	1948	1460	1050	651	388	1219	192	149