Hydrobiologia **355:** 101–113, 1997.
A. D. Naumov, H. Hummel, A. A. Sukhotin & J. S. Ryland (eds), Interactions and Adaptation Strategies of Marine Organisms.

Soft-bottom macro invertebrate fauna of North Norwegian coastal waters with particular reference to sill-basins. Part one: Bottom topography and species diversity

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Key words: Northern Norway, sill-fjords, soft bottom benthos, diversity

Abstract

The soft bottom macrofauna of three fjords in Northern Norway is presented and compared. One fjord is open, with gradually decreasing water depth from mouth to head, and two fjords possess shallow sills, splitting the fjords into two and three basins respectively. The most southerly samples were collected from Rombaken in the innermost part of the Vestfjord, at approximately 68° 23′ N; 17°32 ′ E, close to the city of Narvik. The northernmost samples were collected from Akkarfjord at 70° 46′ N; 23°25 ′ E, near North Cape, Europe's northernmost tip.

The ten numerically most abundant taxa at each station are listed, together with a description of bottom topography, sediment composition and the extent of anthropogenic impact on the fjord. Data are presented on species diversity related to water depth, sedimentary TOC content and presence/absence of shallow sill(s). The dominant faunal groups present are the Polychaeta and Mollusca. In sill basins echinoderms are absent or poorly presented. Species composition generally appears to be most influenced by bottom topography and sediment composition. Waste discharge appears to have only local effects on the faunal assemblages investigated. The TOC content of the bottom sediments tends to increase from exposed, outer parts to the landward parts near the head of the fjord basins. Faunal diversity decreased from open areas (mouth of fjords) towards the sill basins.

Introduction

The North Norwegian coastline is characterised by large and deep fjords, often penetrating hundreds of km inland. Rivers drain into the inner parts of most fjords and, particularly in summer, a temperature and salinity gradient is observed in the upper water masses from open coastal areas to the innermost parts of the fjords. Many North Norwegian fjords have one or more shallow sills, which reduce horizontal water exchange along the longitudinal axis of the fjord. Thus, variations in bottom topography and water depth at the sill (sill depth) between fjords lead to very different water exchange conditions from one fjord to another. It has been shown that sill depth is an important feature regulating the hydrographic conditions of fjords in Western and Central Norway (Aure & Stigebrandt, 1989).

Total or partial renewal of the water in North Norwegian sill basins normally takes place during autumnal/winter inflows of denser coastal water, when passage over the sills is facilitated by the weakening of the stratification as a result of the cooling of the surface waters and the reduced fresh water inflow from the rivers (Eilertsen et al., 1981). However, in some fjords the basin water (the water mass below the sill depth on the landward side of the sill) may not be renewed every year. Over such periods, basin water can potentially become hypoxic or even anoxic due to oxygen-consuming degradation of organic material, but it has been suggested that sub-pycnocline hypoxia is unlikely to occur naturally in Northern Norway (Oug, 1988), and that total renewal of basin water and vertical mixing normally takes place all the way down to the bottom every year. The validity of this suggestion is discussed further in the article.

As decomposition of organic material proceeds in the basin, the oxygen content of the bottom water is reduced during the stagnant period. Minimum oxygen levels are often recorded in August or September. A puzzling observation, made in several fjords, is the presence of a high level of organic material in the bottom sediment, and at the same time a rich benthic fauna and high level of oxygen in the bottom water (present work and own unpublished observations). The present article will introduce the benthic macrofauna of two different fjord environments, with and without sill(s), illustrated by data from three fjords. Further, the diversity of the soft bottom fauna at 54 stations from 14 fjords is related to topographic features in order to describe the general effects of bottom topography on the faunal diversity.

Materials and methods

Survey area

The coastal waters of northern Norway are influenced by the Norwegian coastal current, which flows in a north-easterly direction along the Norwegian west coast. The salinity of the coastal waters varies between 33 and 34.5‰ and the surface water temperature varies from approx. 3 °C in winter (March) to 10 to 12 °C in July/August. The continuous inflow of water from lower latitudes is responsible for all-year ice free conditions in the outer coastal waters of Northern Norway.

The location of the investigated fjords is shown in Figure 1. Faunal data are presented from Akkarfjord with no sills, Rombaken with one shallow sill and Kvænangen with two shallow sills. The longitudinal section of bottom topography in each fjord is obtained from the official sea charts.

Akkarfjord is a relatively small (4 km long) fjord oriented along a northwest-southeast axis with the mouth facing southeast with a sill-free connection towards Sørøysund and the Barents Sea (Figure 2). The bottom topography is relatively flat, with only a few m difference between the innermost parts and the mouth. At the time of the survey (June 1990), two fish farms producing Atlantic salmon were located at the southern bank of the fjord, south of station 2. The fish farms had been in operation for eight and five years respectively. Sludge from a fish processing plant (1000 ton yr^{-1}) had been dumped in the fjord west of station 1 for nearly 50 years.

Rombaken with Rombaksbotn is the inner part of the more than 200 km long Vestfjord/Ofotfjord complex (Figure 3). This very deep fjord (345 m) is located north of the city of Narvik and is approximately 25 km long. The eastern part, Rombaksbotn, is separated from Rombaken by an 18 m deep sill. The basin depth in Rombaksbotn is 113 m. Rombaken receives approx. 12 000 person equivalents (pe.) of municipal waste from the city of Narvik, and approx. 3000 pe. of seepage from a municipal rubbish dump. Both discharges are located on the southern bank of the fjord, at approx. 25 m depth. In December 1990, four stations (G1–G4 in Figure 3) were sampled at intermediate depths (18–35 m) along the southern bank of the fjord. In July 1992, four stations were sampled along the central longitudinal axis of the fjord (stations 4, 5, 6 and 13 in Figure 3).

Kvænangen is a more than 80 km long fjord with several side fjords and branches (Figure 4). Kvænangen is oriented along a northwest-southeast axis. Two shallow sills (7 m and 3 m) separate the fjord into three distinct basins and, furthermore, a relatively deep sill (160 m) separates the fjord from the open sea. Kvænangen has a maximum depth of 200 m, and the two basins have maximal depths of 108 m and 56 m, respectively. In September 1990, four stations were sampled in the deepest parts of the three fjord basins in Kvænangen (Figure 4). The area around Kvænangen is very sparsely populated, and only insignificant amounts of sewage are discharged to the fjord. The catchment area of Inner Kvænangen is 800 km^2 and the precipitation from 40% of this area is conveyed to the fjord through a hydroelectric plant. Inner Kvænangen is normally ice-covered from December to mid-May. The release of fresh water through the power plant during winter increases the duration of the ice cover, and increases the thickness of the ice.

Sediment samples

Samples of surface sediment (0–1 cm) for analysis of total organic carbon (TOC) and sediment grain size were collected using a 0.1 m^2 lead weighted Van Veen grab with hinged, lockable rubber covered inspection flaps of 0.5 mm mesh size. From one grab sample, the top cm of the sediment was sampled. Grain size was determined as fraction of coarse (i.e. >0.063 mm) and fine (i.e. <0.063 mm) particles by wet sieving and weighing each fraction. TOC was determined by two different methods. The samples from Rombaken (1992) were analysed by a method where a dry sample was burnt in oxygen saturated helium gas at approx. 1800 °C. The amount of organic carbon in the initial sample was calculated from the amounts of N_2 and

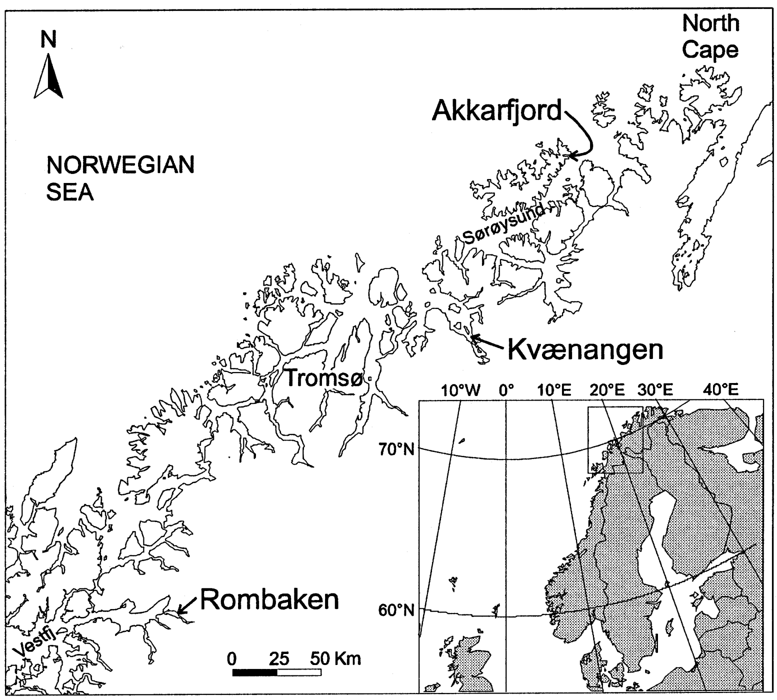

Figure 1. Location of Akkarfjord, Kvænangen and Rombaken, Northern Norway. In addition, material from Beisfjord (1992), Herjangen (1992), Gratangen (1989), Selfjord (1990), Kaldfjord (1990), Ramfjord (1994), Sørfjord (1994), Tverfjord (1989), Stjernsund (1993), Altafjord (1994) Rypefjord (1995) and Forsøl (1995), all located within the indicated area, is included in the delta depth – diversity regression (Figure 5).

CO_2 produced. The sediment samples from Rombaken (1990), Kvænangen and Akkarfjord were analysed by a Leco IR carbon analysator, which measures the amount of CO_2 produced after burning the HCl washed sample at 480 °C.

Fauna samples

The fauna samples were collected using a 0.1 m^2 lead weighted Van Veen grab with hinged, lockable rubber covered inspection flaps of 0.5 mm mesh size. At most stations four replicates were taken (Table 2). All fauna samples were sieved through a 1 mm round hole screen. Material larger than one mm was then preserved in 4% formaldehyde solution, stained with rose bengal. Upon return, the animals were sorted out from the remaining detritus, identified and counted.

The ten numerically most abundant (top-ten) benthic macroinvertebrate taxa are presented from each station. The density of animals per m^2 was calculated for each station. Only benthic, individually living, macrofauna are included, leaving out groups like Foraminifera, Bryozoa and colonial cnidarians, together with copepods, euphausiids and fish. The macrofauna has been identified to the lowest possible taxon, preferably species. For each station, the total number of individuals and taxa were recorded, and the Shannon-Wiener diversity index H' (Shannon & Weaver, 1949) and ES_{100} (Hurlbert, 1971) are presented.

The faunal diversity differences are illustrated by plotting the Shannon-Wiener index vs. delta depth (the difference between the sampling depth at the station and the deepest passage from the station towards the open ocean (Buhl-Jensen, 1986)), this being an index of vertical openness between a station sampled and the open sea.

A clustering analysis is used to illustrate the differences in faunal composition among the stations.

Results and discussion

Investigated fjords

Akkarfjord

The sediment at the three sampling stations consisted of coarse sand, with low TOC content (Table 1). The benthic macrofauna communities were rich in species and

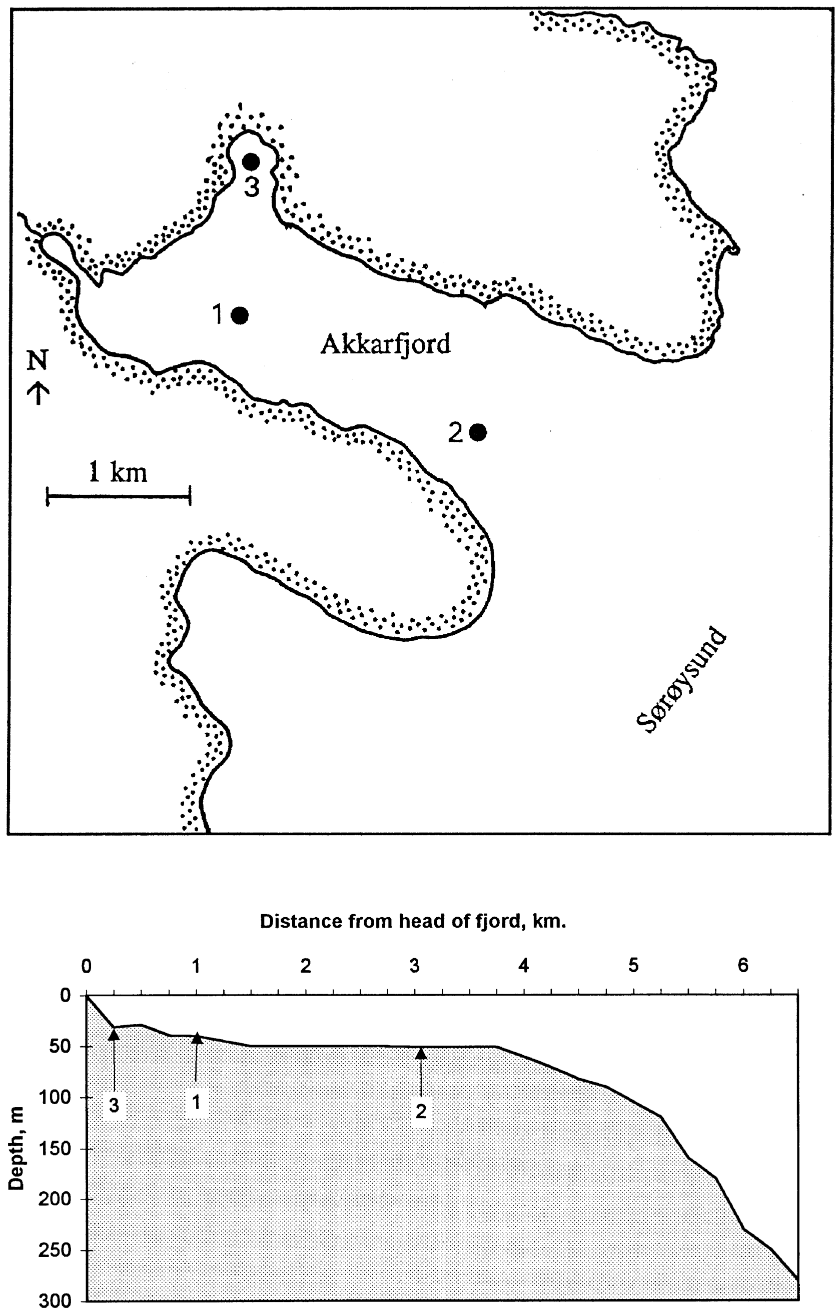

Figure 2. Location and bottom topography along the central axis of Akkarfjord with the three sampling stations indicated.

individuals. The diversity was high at all three stations (Table 2) and the values were well above the lower limit for normal diversity ($H' > 3.1$) according to Norwegian environmental quality criteria (Rygg & Thélin, 1993). Twenty-one different taxa were recorded among the top-ten at the stations in Akkarfjord (Table 3). Eleven taxa belonged to the annelids (all polychaetes), together with 3 crustacean taxa, 3 molluscs, 2 echinoderms, 1 sipunculid and 1 cnidarian.

The most abundant species at station 1 was the burrowing tanaid crustacean *Apseudes spinosus* M. Sars (Table 3). However, this species was not among the ten

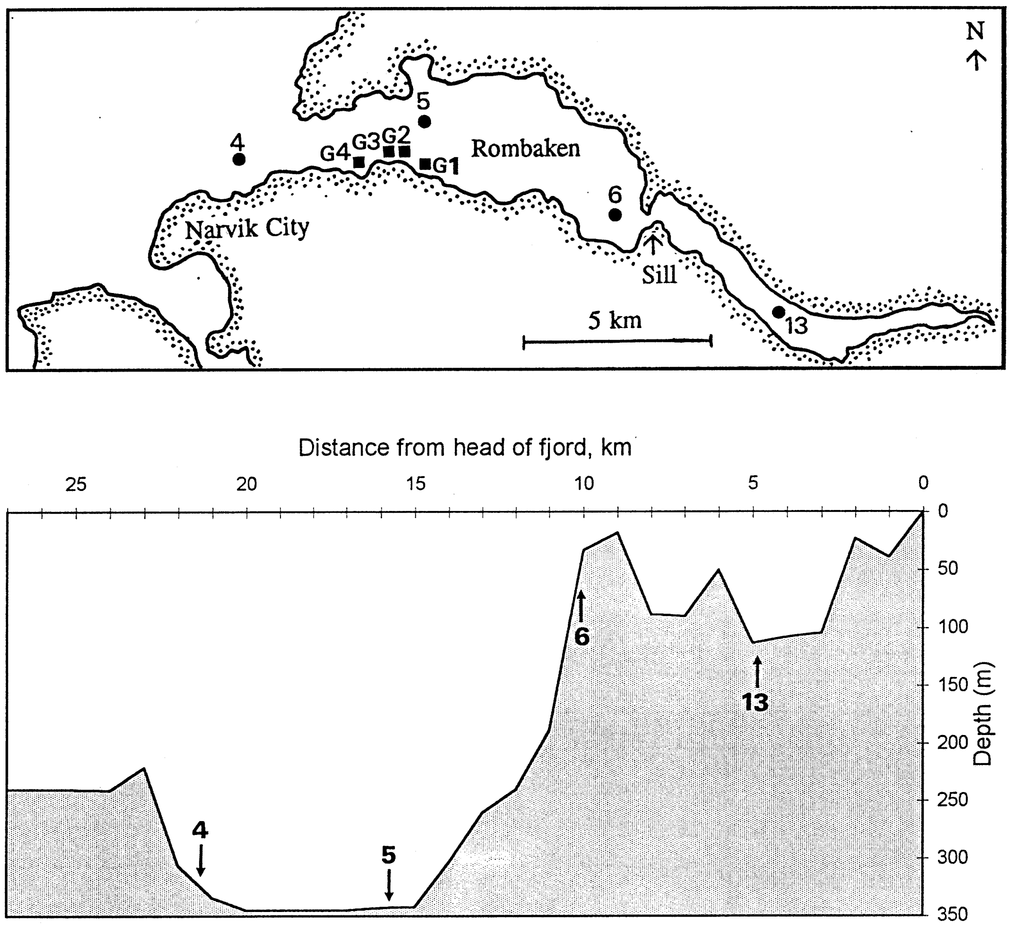

Figure 3. Location and bottom topography along the central axis of Rombaken with the eight sampling stations and the sill indicated. Stations sampled in December 1990 are marked with black squares (G1–G4), while stations sampled in July 1992 are marked with black circles.

most abundant taxa at station 2, and was not recorded at station 3 at all. The most numerically abundant species at station 2 was the polychaete *Onuphis conchylega* M. Sars, which also was recorded among the ten most abundant taxa at station 1, but was not found at station 3 at all. Another polychaete, the sub surface deposit feeding *Scoloplos armiger* O. F. Müller was recorded in highest numbers at station 3, while still another polychaete, the deposit feeding *Chaetozone setosa* Malmgren was the only species recorded among the ten dominant taxa at all the three stations in Akkarfjord (Table 3).

Rombaken and Rombaksbotn

In the 1990 survey, the station G1 was located less than 20 meters from the discharge point for the seepage from the municipal rubbish dump, but the sediment composition and sediment characteristics differed only slightly from the other three stations of that survey (Table 1), located with increasing distance from the outlet. Moreover, compared to the stations of the 1992 survey, the TOC content at G1, G2 and G3 is at the same level (Table 1).

The bottom sediment at the deeper stations (4 and 5 of the 1992 survey) in Rombaken was finer, and had a higher TOC content compared to the intermediate depth station 6 of the same survey, while station 13 had the highest TOC content and the finest sediment of the 1992 stations.

The stations sampled in 1990 had high faunal diversity, even the station G1 located closest to seepage outlet. This station had, however, the lowest diversity of the four stations sampled in 1990 (Table 2), but was still well above the lower limit for normal diversity

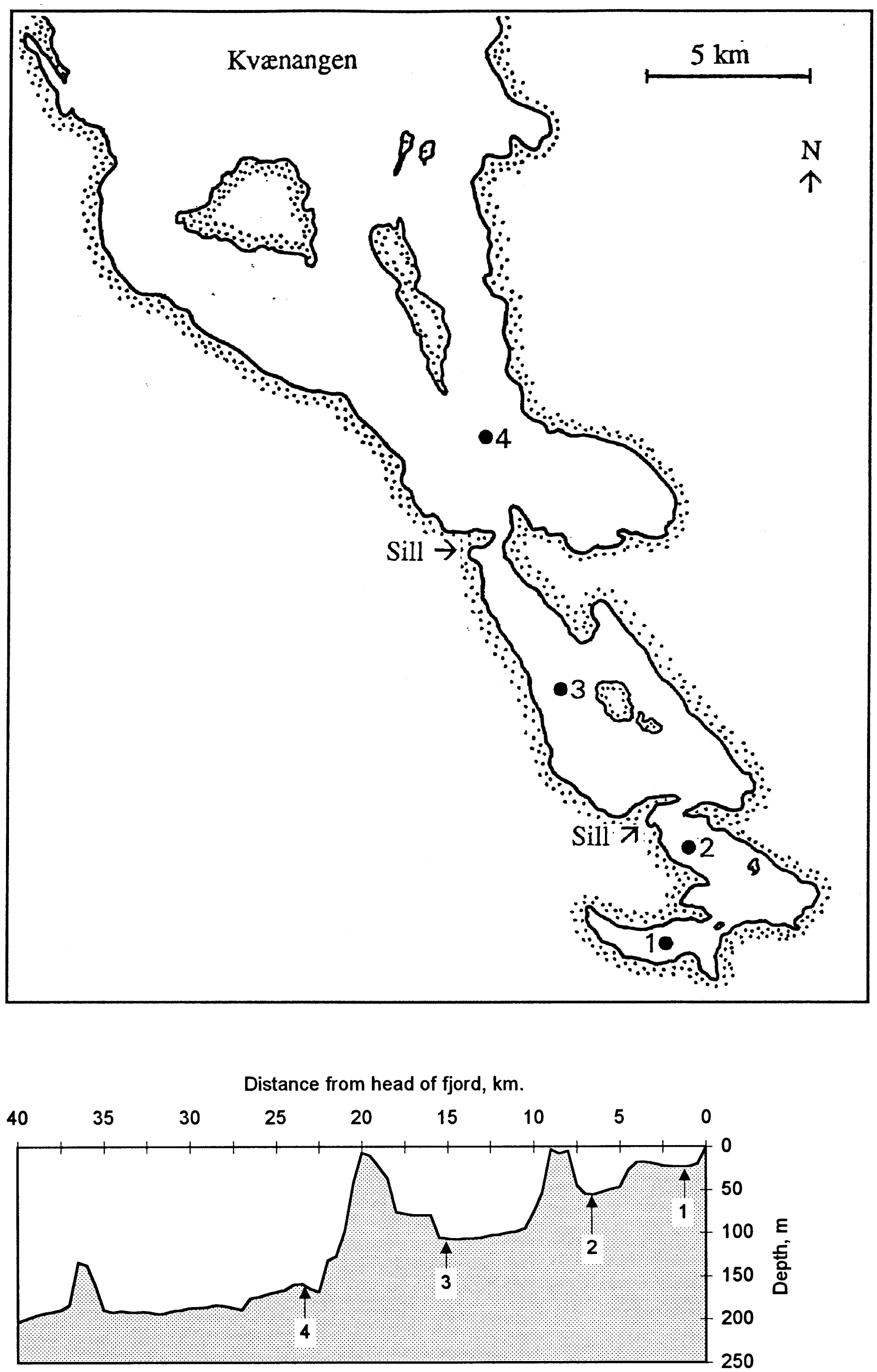

Figure 4. Location and bottom topography along the central axis of Kvænangen with the four sampling stations and the sills indicated.

(H'>3.1) according to Rygg & Thélin (*op cit.*). Of the two deep water stations in the 1992 survey, which had lower diversity compared to the intermediate depth stations, and the station in Rombaksbotn (13) only the latter fell below the quality criteria defined in Rygg & Thélin (*op cit.*). Station 13 had the lowest H' and ES_{100}, and at the same time the highest number of individuals per m^2 of all stations in Rombaken (Table 2).

Table 1. Description of the bottom sediments at the three stations in Akkarfjord, June 1990, the eight stations in Rombaken (December 1990 and July 1992) and the four stations in Kvænangen September 1990.

Station	Water depth (m)	Total Organic Carbon (%)	Pelite (%) ∗	Sand (%) ∗∗	Sediment description
Akkarfjord 1	40	0.8	11	74	Coarse sand with some pebbles and frag-ments of bivalve shells and chalk incrusted redalgae *Lithotamnion* sp. No smell
Akkarfjord 2	56	0.6	5	94	as above
Akkarfjord 3	32	0.5	7	91	as above
Rombaken G1	35	0.8	9	87	Grey sand with fragments of shells covered by a 2-3 mm brown surface layer. No smell
Rombaken G2	18	0.5	n.d.	n.d.	Muddy sand without smell
Rombaken G3	28	0.9	18	82	Muddy sand with shell fragments, no smell
Rombaken G4	25	1.2	9	52	Muddy sand with a lot of shell fragments. No smell
Rombaken 4	311	1.1	63	34	One cm of light brown surface layer upon blue-grey clay. No smell
Rombaken 5	350	1.1	77	23	One cm of light brown surface layer upon blue-grey clay. No smell
Rombaken 6	37	0.3	28	64	Grey sand/stones and fragments of bivalve shells. No smell
Rombaken 13	113	1.7	82	18	Dark brown silt without smell.
Kvænangen 1	24	1.2	82	18	Dark grey silt. Black below 3 cm depth, weak smell of H_2S from deeper parts. Some shell fragments and polychaete tubes on the surface.
Kvænangen 2	56	1.6	78	22	Dark fine silt, deeper than 2 cm black mud. Weak smell of H_2S
Kvænangen 3	108	1.3	52	47	Brown-grey clay-silt. No dark coloration and no smell
Kvænangen 4	103	0.7	38	62	Fine greyish sand with some shell fragments. No smell.

$*$ = Σ particles $< 63\ \mu$m.
$**$ = Σ particles $> 63\ \mu$m and < 2 mm.
n.d. = not determined.

Station 6 of the 1992 survey had a species diversity comparable to the stations of the 1990 survey (Table 2), which can be explained by comparable water depth and sediment composition (Table 1). At the four stations sampled in Rombaken in 1990, twenty-three different taxa were recorded among the top ten at one or more stations (Table 4), while the number was twenty-six for the stations sampled in 1992. Station 6 of the 1992 survey had 5 'top-ten' list taxa in common with the stations of the 1990 survey, which is not surprising when comparing location, depth and sedimentary conditions (Table 1). The two deep stations of the 1992 survey only had the deposit feeding polychaete *Prionospio cirrifera* Wirén in common with the stations from 1990 and station 6 from 1992. The fauna at station 13 was strongly dominated by the tube dwelling oweniid polychaete *Myriochele oculata* Zachs. This species alone made up 66% of the total number of individuals recorded at this station (Table 2). The fauna at station 13 only had three 'top-ten list' species in common with the deep-water stations on the sea-ward side of the sill (Table 4). The polychaetes are the numerically dominant group in the intermediate depth coarse sediment stations (G1–G4 in 1990 and 6 in 1992), where they made up 15 of 23 taxa in the 1990 survey and 7 of 10 taxa at station 6 in the 1992 survey. In the deeper, fine sediment relatively TOC rich stations on the sea-ward side of the sill (4 and 5, 1992) the polychaetes made up 4 of 12 taxa at the top-ten list, while bivalve molluscs dominated with 6 different bivalve species represented at the top-ten list (Table 4).

Kvænangen

The sediment gradually got coarser when moving from the innermost station (1) to the outermost (4), despite the increasing water depth (Table 1). The three innermost stations in Kvænangen all have H' values around the lower limit for the classification 'good environ-

Table 2. Total number of benthic macrofauna-taxa and individuals recorded per station, together with diversity indices (H' and ES_{100}) at the three stations in Akkarfjord, June 1990, the eight stations in Rombaken December 1990 and July 1992, and the four stations from Kvænangen, September 1990.

Station	Sampled area	Number of taxa	Number of individuals	Number of individuals per 1 m^2*	ES_{100}	H'
Akkarfjord 1	0.4	148	1129	2823	45.6	5.70
Akkarfjord 2	0.4	133	740	1850	51.5	6.04
Akkarfjord 3	0.1	58	200	2000	40.0	5.01
Rombaken G1	0.4	88	967	2418	33.2	4.83
Rombaken G2	0.3	96	670	2231	43.2	5.49
Rombaken G3	0.4	111	1285	3213	42.9	5.56
Rombaken G4	0.4	125	1440	3600	43.1	5.52
Rombaken 4	0.4	83	1315	3288	27.1	4.29
Rombaken 5	0.4	53	1163	2908	23.4	3.98
Rombaken 6	0.4	107	938	2345	41.6	5.40
Rombaken 13	0.4	47	1788	4470	14.0	2.22
Kvænangen 1	0.4	46	606	1515	20.3	3.15
Kvænangen 2	0.4	41	801	2003	16.2	3.04
Kvænangen 3	0.4	85	2258	5645	19.7	3.08
Kvænangen 4	0.4	92	1015	2538	33.5	4.57

∗ Calculated values

mental quality' according to Rygg & Thélin (*op cit.*) (Table 2). The faunal assemblages were rich in individuals, particularly at station 3, where the polychaete *M. oculata* made up 44% of the more than 5500 individuals per m^2 (Table 2).

Twenty-seven different taxa are recorded among the 'top-ten' at one or more of the stations in Kvænangen. Fourteen taxa were annelids (all polychaetes), while 6 mollusc taxa, 4 crustacean, 2 echinoderm and 1 cnidarian taxa were found (Table 5). The polychaete dominance in the Kvænangen material was most pronounced at station 2 and 3, while relatively few polychaetes (3 taxa) were recorded at station 1 and 4. *M. oculata* was the most abundant species, and together with a species of the bivalve family Thyasiridae, it was the only taxon occurring at all four stations (Table 5).

Importance of human impact

The human impact on the North Norwegian fjords arises mostly from discharges of organic effluents from sewage, aquaculture, dumping of fish processing waste and from fishing and manipulations of the hydrographic regime through operation of hydroelectric power stations. The latter increase the formation and duration of ice-cover on the inner parts of the fjords. The discharges generally affect the organic content of the sediments directly by adding organic material or nutrients. The fishing activities do not exert any direct physical impact to the bottom communities, as the use of trawls is prohibited, and the major impact arises form the manipulation of the biomass of benthic feeding fish like cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), and different flatfish species. The data in the present article have been collected in the course of environmental monitoring studies, assessing the human impacts on the fjord environments, which is reflected in the location of the stations.

Rombaken and Akkarfjord are the fjords which at the time of the surveys received the largest direct anthropogenic discharges, but still the faunal diversities were high. Even station G1 in Rombaken, located twenty meters from a discharge of 3000 pe seepage had high species diversity, and normal TOC content in the sediment. Station 4 of the 1992 survey is located some 200 m from the discharge of 12 000 pe of sewage, and still maintains a faunal diversity higher than at station 5, located outside the expected range of any discharges. Station 13 in the sill basin Rombaksbotn is located more than 10 km from any major discharges, but has still the lowest species diversity (Table 2). Thus, comparing the stations in Rombaken, the largest influence

Table 3. The ten numerically most abundant taxa at each station in Akkarfjord (June 1990) with number of specimens per m^2.

Taxon	Akkarfjord 1	2	3
Polychaeta:			
Chaetozone setosa	172	80	150
Nereimyra punctata	134	70	
Harmothoe imbricata	100		50
Typosyllis armillaris	70		
Owenia fusiformis		85	
Scoloplos armiger		73	220
Euclymene praetermissa		48	130
Pholoe minuta			170
Spio filicornis			170
Goniada maculata			60
Onuphis conchylega	92	170	
Mollusca:			
Ichnochiton albus	70		
Macoma calcarea			90
Thyasira spp			60
Echinodermata:			
Ophiura robusta	154	48	
Ophiopholis aculeata	160	43	
Crustacea:			
Urothoe elegans		93	
Apseudes spinosus	398		
Ostracoda indet.	68		
Sipunculida:			
Phascolion strombi		68	
Cnidaria:			
Cnidaria indet.			110
Top ten% of total	50.2	42.1	60.5

on the species composition and the diversity of faunal assemblages seems to be exerted by the fjord bottom topography, e.g. presence or absence of a shallow sill, compared to the recorded anthropogenic discharges.

Generally, organic input will act as a fertiliser, stimulating an increase in the populations of benthic macrofauna, but comparing the fauna of station 13 in Rombaksbotn with station 3 in Kvænangen (both behind one sill, water depth 113 and 108 m resp.) receiving almost no anthropogenic discharges, reveals a nearly identical faunal density and diversity and the highest faunal densities among all stations (Table 1 and 2). This indicates that the stimulating effect from organic discharges has less influence on faunal density than the presence of a shallow sill.

Kvænangen receives only insignificant amounts of sewage, and the discharge from a minor aquaculture plant to the inner part of the fjord is the only anthropogenic input of organic material. The two stations in Inner Kvænangen (1 and 2) had low numbers of taxa, but approximately the same number as station 13 in Rombaksbotn (Table 2). At station 3 in Kvænangen, nearly twice as many taxa were recorded compared to the station in Rombaksbotn (Table 2). The polychaete *M. oculata* dominated the fauna both at station 3 in Kvænangen and station 13 in Rombaksbotn. The sedimentary conditions in Rombaken were comparable to station 2 in Kvænangen, while station 3 in Kvænangen had a somewhat coarser sediment.

Characteristics of the fauna in fjord basins

On basis of the faunal assemblages at the investigated stations a cluster analysis was made (Figure 5). The results are similar when all species are included (Figure 5a), or when only the top ten species are included (Figure 5b). The largest similarity in species composition is seen among stations in the same fjords, and in each fjord the sill basin stations form individual clusters. Only station 6 in Rombaken falls outside this pattern, with a fauna more comparable to the fauna recorded in Akkarfjord (Figure 5).

Thus, the data presented from the three North Norwegian fjords show marked differences in fauna diversity. Inter fjord comparison reveals that only four taxa are common for the top-ten lists from Akkarfjord and Kvænangen, while 11 species are common for Akkarfjord and Rombaken (Table 4). Kvænangen and Rombaken are both large fjords with a variety of habitats, and should expectedly share a relatively high number of taxa at the top-ten lists. However, only 7 taxa are shared by these two large fjords (Table 4 and 5). The dominant groups of animals in sill basins are polychaetes and bivalve molluscs, while the echinoderms, which are strongly represented in outer parts of the fjords, are very poorly represented in the sill basins. No echinoderms are among the dominant taxa at the station in Rombaksbotn (13), and a single specimen of the mud sea star *Ctenodiscus crispatus* (Retzius) was the only echinoderm in the entire material. In Kvænangen, only station 4 on the sea ward side of the sills had echinoderms represented at the top-ten list. The oweniid polychaete *M. oculata* has a nearly alternating dominance compared to the echinoderms, and is recorded in great numbers in the sill basins in Kvænangen and Rombaksbotn, but is less represented

Table 4. The ten numerically most abundant taxa at each station in Rombaken (December 1990 and July 1992), with number of specimens per m^2.

	Rombaken 1990				Rombaken 1992			
Taxon	G1	G2	G3	G4	4	5	6	13
Polychaeta:								
Chaetozone setosa	223		148	148				308
Onuphis conchylega		130					125	
Owenia fusiformis			73				183	
Scoloplos armiger	305	57	183	123				40
Pholoe minuta		107	150	140				
Spio filicornis	80							
Goniada maculata	90	53						
Tauberia gracilis	378							
Myriochele oculata	128	117	350				245	2963
Prionospio cirrifera	85	263	158		100	423	55	55
Capitella capitata	70							
Nephtys ciliata			145	153				
Petaloproctus tenuis			113	118				
Cossura longocirrata				103				
Heteromastus filiformis					773	668		153
Asychis biceps					70	80		
Streblosoma intestinale						63		
Spio decoratus							265	
Myriochele danielsseni								95
Melinna cristata							88	
Maldane glebifex								270
Sabellidae indet.		60	85				130	
Mollusca:								
Macoma calcarea				465				
Astarte montagui	83							
Parvicardium minimum		173						
Thyasira obsoleta					398	120		
Thyasira minuta					328	365		138
Thyasira equalis					218	285		150
Thyasira eumyaria						70		
Abra nitida					193	110		
Nucula tumidula					123			
Cardium minimum							60	
Echinodermata:								
Ophiura robusta		140	165	378				
Labidoplax buskii					65			
Echinus sp.				118				
Crustacea:								
Hemilamprops rosea							48	
Leuchon nasica								48
Apseudes spinosus				108				
Diastylis sp.							80	
Ostracoda indet.		63						
Nematoda:								
Nematoda indet.	153							
Sipunculida:								
Onchnesoma steenstrupi					275	168		
Top ten% of total	66.0	52.1	48.9	51.5	77.3	80.9	54.5	94.4

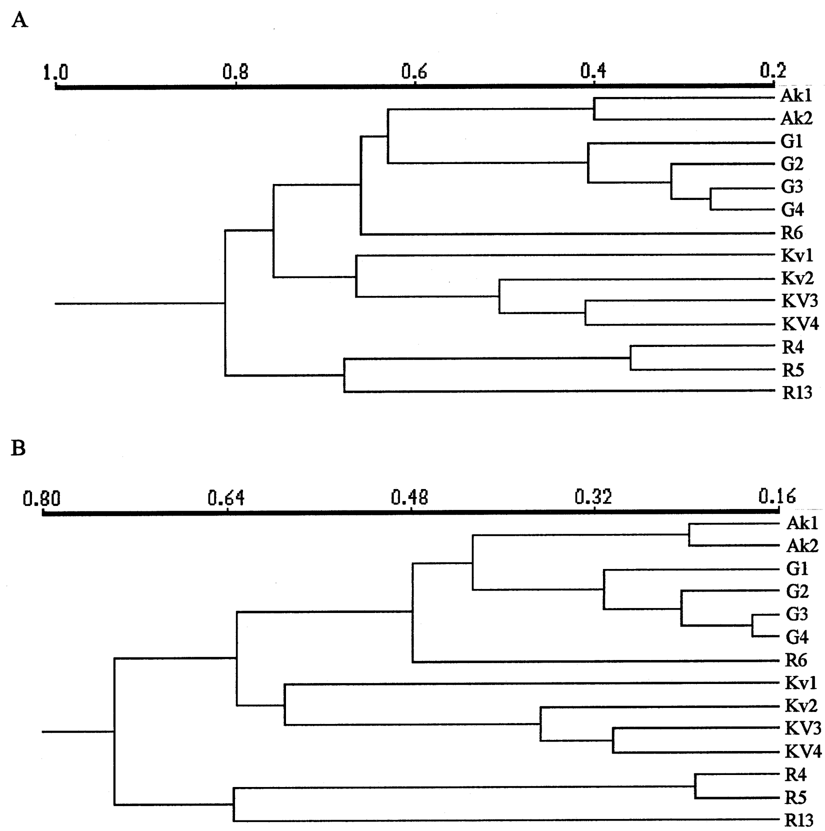

Figure 5. A: Dendograms of the classification of the faunal assemblages at the 14 stations in Akkarfjord (Ak1, 2), Kvænangen (Kv1–4) and Rombaken (G1–G4 and R4, 5, 6, 13), Northern Norway, based on Bray-Curtis similarity measures and group average sorting. A: All species included, matrix correlation $r = 0.913$, B: only top 10 species included, matrix correlation $r = 0.883$.The stations Kv1–3 and R13 are located in sill basins. Station 3 in Akkarfjord, consisting of only one grab sample, is excluded. The horizontal axis indicates dissimilarity (value 0 = total similarity, value 1 = no species in common, total dissimilarity).

in outer fjord areas. In Akkarfjord, *M. oculata* was not recorded at all, while this species was dominant at three of four stations in Kvænangen (Table 5).

The bottom topography of the fjords exerts a major influence on water exchange and sedimentation conditions, which in turn is permissive for the species composition and macrofauna diversity. In the two sill basins presented, H′ index attained a value of around or less than three, while sill free areas are characterised by higher diversities (H′ normally above 4). The values of the ES_{100} shows the same variation as the H′, generally with values below 20 for stations in sill basins, and values above 20 for stations on the seaward side of the sills (Table 2). The general validity of the influence exerted by the presence of a sill is illustrated in Figure 6. This shows the diversity at 52 stations sampled in 14 different fjords (Figure 1) of Northern Norway as function of ‘topographic isolation’ (delta depth sensu Buhl-Jensen (1986)) of the stations. The topographic isolation is calculated as the difference between the depth of a sampling station and the depth of the deepest passage from the station to the open sea. Sampling stations in fjord basins on the landward side of shallow sills will appear to the right along the x-axis (Figure 6). The correlation is significant ($n = 52$, $r = -0.57$, $p < 0.001$). The diversity H' attains a value of between 4 and 6 for open area stations. These stations are all located near the left vertical axis in Figure 6. Stations at intermediate depths in sill basins should seem to take values for H' of between 3 and 4, while stations in deeper parts of sill basins have H' values around 3 and lower. The tendency towards reduced diversity in sill basins compared to open sea sites has been described for fjords of western Norway by Buhl-Jensen (1986), working on amphipods and by Buhl-Mortensen & Høisæter (1993) working on molluscs. A much stronger correlation is

Table 5. The ten numerically most abundant taxa at each station in Kvænangen (September 1990), with number of specimens per m^2.

Taxon	Kvænangen 1	2	3	4
Polychaeta:				
Chaetozone setosa			173	
Onuphis conchylega				324
Owenia fusiformis	43			
Scoloplos armiger				87
Myriochele oculata	98	946	3326	1006
Prionospio cirrifera				107
Nephtys ciliata		24		
Maldane sarsi	693	266	1449	
Pectinaria koreni		204		
Lumbrineris fragilis		150	230	
Laphania boecki		31	230	
Sabellides borealis			124	
Myriochele heeri			133	
Praxillella sp.		27		
Mollusca:				
Astarte montagui	45			
Musculus niger	38			
Yoldiella fraterna				58
Yoldiella sp.				98
Thyasira spp.	33	477	88	128
Caudofoveata indet.		80	65	
Echinodermata:				
Labidoplax buski				118
Ophiura sp.				65
Crustacea:				
Eudorella emarginata	33			
Diastylis rathkei	255			
Bathymedon obtusifrons	43			
Protomedeia fasciata	30			
Cnidaria:				
Anthozoa indet.	0	20	215	65
Top ten% of total	86.6	90.6	81.9	66.0

recorded between delta depth and diversity in fjords of Western Norway compared to the present material (Buhl-Jensen 1986). This might indicate a generally better water exchange in North Norwegian fjords, compared to western Norway, allowing a more diverse fauna in deeper sill basins.

The fauna recorded in the sill basins of the present survey includes several long lived species like e.g. *Maldane sarsi*, a dominant in the Kvænangen material, but also the *Sabellides borealis* and *Lagis (Pectinaria) koreni* Malmgren have a life span covering more than one year. The presence of these organisms indicates that hypoxia is unlikely to have occurred in the investigated sill basins during the latest years prior to the surveys. During sampling of the sediment and fauna at all fifteen stations, a smell of H_2S from the sediment was only recorded once. This observation, together with the records of large, deep burrowing macrofauna, also indicates that hypoxia or anoxia is unlikely to have occurred.

However, the low number of echinoderms, which generally are sensitive to hypoxia, recorded in the sill basins indicates that sub-pycnocline hypoxia might occur naturally in the fjords. On the other hand, the distribution pattern of the echinoderms might be influenced to a larger extent by the sedimentary conditions than by the oxygen contents of the water column, and can thus not be used as evidence for occurrence of hypoxia. Besides facilitating the summer stratification, the outflow of fresh water causes a general reduction in salinity in the upper layers of the water column, and the absence of echinoderms in the sill basins might be due to the lower salinity of the upper waters, being lethal to the echinoderm larvae. However, the present material does not allow a thorough investigation of this suggestion.

Buhl-Mortensen (1994) concludes that the most important feature, leading to a reduced diversity in molluscs and amphipods in sill basins is the finer grain size of the sediment, arising due to the sill's reduction of current speed, which in turn leads to a less heterogeneous sediment with less different habitats. Hampering the water exchange, a sill is also responsible for the keeping of stagnant basin water in sill basins.

Besides the generally cooler summer and thus less heating of the surface water in Northern Norwegian fjords compared to the fjords of Western Norway, the tidal amplitude is larger in Northern Norway. Average tidal amplitude in Narvik is 182 cm, compared to 90 cm in Bergen, Western Norway. The tidal water exchange is thus a factor contributing to a larger exchange of water in North Norwegian fjords, and an expected shorter duration of a stagnant situation during summer.

In conclusion, the investigations of the benthic macrofauna of three North Norwegian fjords indicate, that the bottom topography exerts a far larger influence on the species composition and species diversity in sill basins, compared to anthropogenic discharges of sewage. The results also indicate that hypoxia or anoxia is unlikely to have occurred in the investigated sill basins the latest two–three years before the surveys.

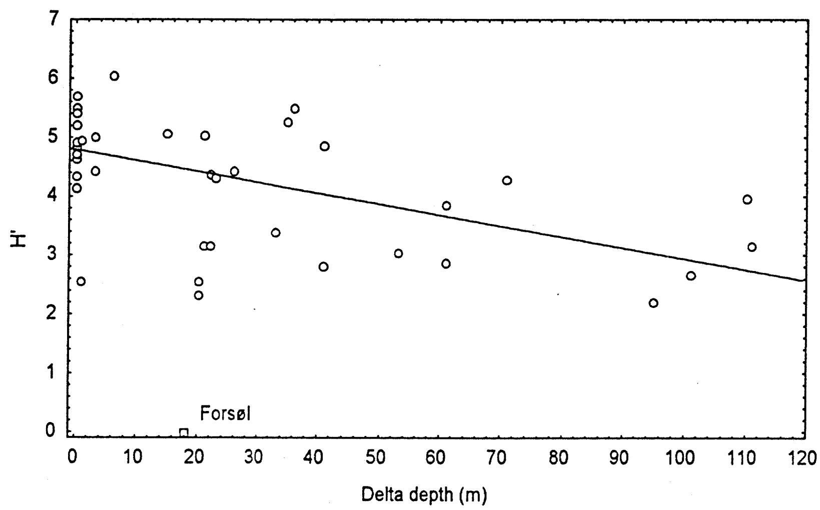

Figure 6. Benthic macrofaunal diversity (H') versus delta depth (index of topographic isolation) for 52 stations in coastal areas of Northern Norway (regression line: $y = 4.8 - 0.019x$; $r = -0.57$, $p < 0.001$).

Acknowledgments

The material has been collected by Akvaplan-niva in connection with a number of different commissions, each with a specific purposes and extent. All material has been reported to the commissioners in Norwegian. Field work, identification and treatment of the material has been carried out in co-operation with colleagues at Akvaplan-niva. The compilation and presentation of the results has received financial support from the Norwegian Ministry of the Environment through a grant to Akvaplan-niva. The author is grateful to the following colleagues for carrying out field work, identification, and statistical analyses of the material: Sabine Cochrane, Salve Dahle, Rosie Evans, Reinhold Fieler, Bjørn Gulliksen, Børge Holte, Hans-Petter Mannvik, Rune Palerud, Wim Vader, Roger Velvin, Anders Wàren and Ursula Witte. The manuscript has benefited from constructive comments and suggestions from Eivind Oug, Norwegian Institute for Water Research, and from the anonymous reviewers of the manuscript.

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