

Soft-bottom macrofauna in the high-latitude ecosystem of Balsfjord, northern Norway: Species composition, community structure and temporal variability

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The fjords of northern Norway are generally weakly stratified and subject to frequent large-scale advective water mass exchanges. In Balsfjord, studies of production and trophic relationships have shown that most of the biological production is mineralised in the pelagic food webs, or is exported. This study examines the soft-bottom macrofauna (> 1 mm) in the deep basin of Balsfjord (185 m). Yearly monitoring surveys were conducted from 1977 to 1987, supplemented by samples taken in 1994, to assess long-term changes. Data to assess seasonal changes were obtained in 1979, 1982 and 1994. The fauna was strongly dominated by small annelids comprising 78 species and representing 97 % of the specimens. The numerically dominant species were the polychaetes *Myriochele oculata*, *Levinsonia gracilis* and *Lumbrineris mixochaeta*, and the oligochaete *Tubificoides cuspidatus*. Species numbers ranged from 20 to 59 per survey, densities from 1700 to 9800 ind. m^{-2} and diversities (Shannon-Wiener H'_{log2}) from 1.9 to 3.6. Deposit feeders constituted about 90 % of the specimens, carnivores about 10 % and suspension feeders a small fraction only. During the study period, species numbers and densities increased, while the structure of the community remained largely the same. Seasonal variations were insignificant. It may seem that the species assemblage was dependent on a low, irregular supply of largely low-quality nutrient material. The increasing densities may probably be related to the nutrient dynamics in the fjord, which is significantly influenced by advective exchanges of plankton into and out of the fjord.

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INTRODUCTION

The coastal waters of northern Norway are in the transition zone between boreal and Arctic areas. The coastline is characterised by a number of large, deep fjords with more or less direct connections with the surrounding open sea. Most fjords have rather homogeneous water masses which undergo extensive exchange with the seawater outside. Balsfjord, on the other hand, is a silled fjord with a more limited exchange of deep water. This feature, coupled with climatic factors, results in particularly cold basin water which is amenable to a number of cold-water species. Northern Norwegian silled fjords have long been known as a refuge for Arctic benthic species which appear to have local populations in the inner reaches of the fjords (Kiær 1906; Soot-Ryen 1951). Also, Balsfjord is home to an indigenous stock of the small Arctic pelagic fish capelin *Mallotus villosus* (Müll) (Hopkins & al. 1989).

Since the mid-1970s, Balsfjord has been the subject of a multi-disciplinary research programme studying water masses, plankton dynamics, particle sedimenta-

tion, and commercial fish and shell-fish species (Eilertsen & al. 1981; Klemetsen 1982; Hopkins & al. 1989; Lutter & al. 1989; Hopkins & Nilssen 1990). Most of the studies have been conducted in the central and deepest part of the fjord. The ultimate aim of the studies has been to provide quantitative descriptions of the biological production and the energy flow within the fjord system. The studies have demonstrated that most biological production is mineralised in the pelagic food chains (Hopkins & al. 1989). Little of the production reaches the bottom in the fjord basin. The development and fate of vernal blooms, the transfer of nutrient matter and energy in the pelagic system, and the nutrient fluxes to the bottom, however, are significantly influenced by the advective exchanges of water masses introducing and removing plankton in the fjord (Reigstad & Wassmann 1996).

The present study examines the soft-bottom fauna in the deepest part of the fjord. The data were collected from 1977 to 1994, partly overlapping studies of plankton dynamics and sedimentation. Its objectives are to describe species composition, community structure and

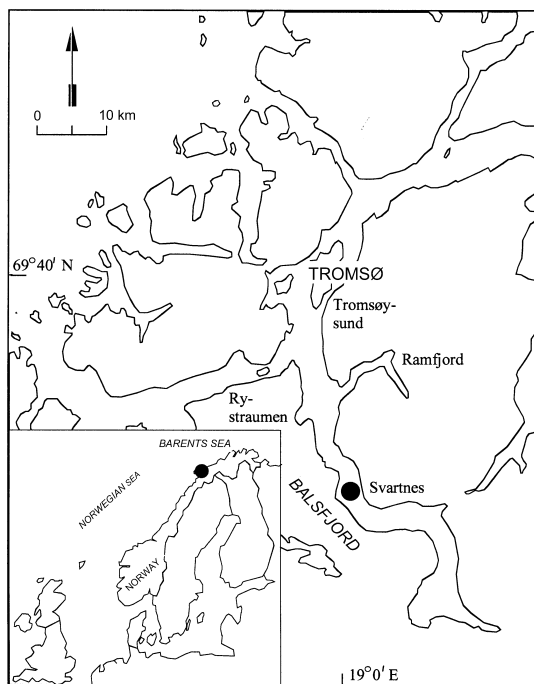


Fig. 1. Balsfjord, northern Norway. The location of sampling station in the fjord basin near Svartnes is indicated.

trophic relationships in terms of seasonal and long-term patterns, and to interpret these in relation to the energy flow and dynamics of the ecosystem. Previous investigations of the soft-bottom fauna in the fjord are restricted to an early faunal survey (Kiær 1906) and a study of the population ecology of the polychaete *Pectinaria hyperborea* (Velvin 1981). The distribution and reproduction of molluscs and echinoderms were the subject of studies in an arm of the Balsfjord, the Ramfjord (Soot-Ryen 1924; Falk-Petersen 1982b, 1982c; Falk-Petersen & Sargent 1982).

STUDY AREA

Balsfjord (69°20'N, 19°0'E) reaches approximately 40 km into the Norwegian mainland, south of the city of Tromsø (Fig. 1). The fjord is separated from the open coastal waters by relatively narrow sounds with sills of 10 and 35 m water depth (Tromsøysund, Rystraumen). The maximum depth is 195 m in the deep basin near Svartnes in the central part of the fjord. The deep basin (180–195 m) is approximately 12 km long and has a flat bottom consisting of finely grained mud.

The temperature of the water masses ranges from 1 to 7 °C, while salinity stays between 32 and 34 psu throughout most of the year (Eilertsen & al. 1981). The fjord

does not have a winter ice-cover. The water column is vertically mixed and almost homogeneous from October until the end of April. In most years, the vertical convection reaches the bottom in late winter. In summer, the water masses are stratified due to freshwater runoff and summer heating of surface waters. Large-scale advective exchanges of water masses, driven by local wind stress and the hydrophysical characteristics of the coastal water masses, may take place frequently. The dominant inflow of deep water takes place during spring. The temperature of the bottom water usually drops during winter due to convection, and increases in spring due to inflows of deep water (Eilertsen & al. 1981; Finne & Gade 1990). The water masses are well oxygenated and oxygen levels do not fall below 70 to 80 % saturation in the bottom water (Eilertsen & al. 1981; Sargent & al. 1983).

The fjord is productive, with the primary production rate exceeding 100 g C m⁻² per year (Eilertsen & al. 1981; Eilertsen & Taasen 1984). Phytoplankton production begins in late March and peaks in April, mainly in weakly to non-stratified surface waters. A second, lower, peak occurs towards the end of the production season in August/September. The majority of the production seems to be mineralised in the water masses through relatively short food chains, running from herbivorous copepods and euphausiids to pelagically feeding fish (Hopkins & al. 1989). Significant amounts of the phytoplankton production may also be exported from the fjord by means of advection. Detritus and euphausiid faecal pellets account for most of the recognisable organic matter that reaches the fjord bottom (Hopkins & al. 1989; Lutter & al. 1989; Reigstad & Wassmann 1996), but the amount and type of sedimenting material is heavily dependent on the extent and duration of advective episodes (Reigstad & Wassmann 1996). The sediments in the deep basin are of low nutritive value, showing almost no seasonal variation in values for organic carbon, nitrogen, amino acids and lipids (Sargent & al. 1983). Indeed, it seems that seasonal production pulses in the upper waters are largely eliminated in the organic material reaching the deepest parts of the fjord.

Deep-water prawns *Pandalus borealis* Krøyer are abundant in Balsfjord. The prawn was the basis for a small commercial fishery in the deep basin until 1983, when the fishery was discontinued because of a ban on prawn trawling in many Norwegian fjords by national legislation (Hopkins & Nilssen 1990). Other than the prawn, the fauna in the water layer immediately above the sediment consists of ordinary zooplankton and a minor component of hyperbenthic crustaceans (Hopkins & Gulliksen 1978; Oug, unpubl.). The presence of a poor hyperbenthic fauna supports the impression that there is a low input of high-quality organic material in the deep basin of the fjord.

MATERIAL AND METHODS

SAMPLING AND ANALYTICAL PROCEDURES

The sampling station was at 185 m in the northern part of the Svartnes basin (Fig. 1). The station was located using landmarks. Samples were collected during 27 cruises from 1977 to 1994 (Table 1). From 1977 to 1987, there was at least one survey per year preferably conducted in the autumn (October to December). In 1979, 1982 and 1994, three to eight surveys were conducted at different times during the year to evaluate seasonal patterns. Usually, four replicate samples were taken in each survey using a 0.1 m² light-weight van Veen grab. The samples were sieved through 1 mm round-holed screens, and preserved in 4 % buffered formaldehyde solution. Most specimens were identified to the species level. Care was taken to standardise sampling and sample processing methods; in particular, all species identifications were performed by the same people.

Samples of surface sediment for analysing organic matter and grain size distribution were collected in 1994 using a reinforced van Veen grab equipped with hinged, lockable rubber-flap-covered inspection windows on the upper surface. Organic matter (0–1 cm layer) was determined as total organic carbon (TOC) and total nitrogen (TN) using a Carlo Erba CHN-analyser after removing inorganic carbonates by acidification. The grain size distribution (0–5 cm layer) was determined according to the Wentworth scale by dry sieving of the coarse fraction (particles > 0.063 mm), and electronic particle counting using a Sedigraph 5100 on the fine fraction (particles < 0.063 mm). The fractions were initially separated by means of wet sieving.

Hydrographical data (temperature, salinity) were obtained by a routine sampling programme using a Neil Brown CTD sonde. Details of the programme may be found in e.g. Finne & Gade (1990).

DATA ANALYSES

The species composition and total densities were determined for each grab sample and each survey. Data for individual grab samples were used to estimate sampling variability, while data for each survey (pooled replicate samples) were used to study seasonal and long-term patterns. Community structure was described using the Shannon-Wiener H' diversity index (\log_2 base). Long-term patterns in the number of species, total density and diversity (H') were tested for statistical significance using the mean square successive difference test (Zar 1984).

Community composition and variability were assessed using correspondence analysis and principal component analysis. Correspondence analysis (CA) was

used to display faunal similarities between samples and to quantify components of species variation. In CA, species variation (referred to as “inertia”) is calculated as a measure of the distribution of species scores along ordination axes. The magnitude of the inertia depends on how well species are separated, and hence reflects the degree of heterogeneity in the data. The total species variation (“total inertia”) may be separated into components of variation within and between groups of samples by performing successive analyses on separate and pooled samples (Greenacre 1993; Fieker & al. 1994). In this study, a series of analyses was performed on, respectively, individual grab samples, pooled data for surveys, and pooled data for years, for the purpose of estimating the amount of species variation attributable to spatial dispersion patterns, seasonal changes and differences between years. Rare species (sum of specimens for all samples < 10) were omitted. Species data were square-root transformed prior to analysis to down-weight high abundances.

Principal component analysis (PCA) was used to evaluate temporal trends and display relationships between species. One analysis (partial PCA) was performed specifically for assessing seasonal patterns (data from 1979, 1982, 1994). In this analysis, the year was entered as a covariable (categorical variable) in order to deduct general differences between the years. The PCAs were restricted to the most frequently occurring species (frequency > 80 %) to avoid problems from zero values and non-linearity in PCA. Species data were log-transformed ($\log(x+1)$) prior to analysis to make species variances homogeneous. CA and PCA were performed with the program CANOCO version 3.10 (ter Braak 1988, 1990). Plots were produced with the drawing program CanoDraw 3.0 (Smilauer 1992).

Table 1. Sampling dates and number of replicate grab samples (in parentheses) taken during each survey in Balsfjord from 1977 to 1994.

Year	Date and number of replicate samples
1977	7 Dec (3)
1978	23 Aug (2)
1979	23 Mar (1), 18 Apr (3), 23 Apr (3), 31 May (4), 31 Jul (4), 24 Sep (3), 10 Oct (4), 10 Dec (4)
1980	19 Mar (2), 2 May (3), 25 Nov (4)
1981	1 Dec (4)
1982	11 Feb (4), 30 Apr (4), 9 Jun (4), 24 Sep (4), 1 Dec (4)
1983	1 Nov (4)
1984	7 Nov (4)
1985	29 Oct (3)
1986	26 Nov (4)
1987	1 Dec (4)
1994	24 Jan (4), 13 Sep (4), 13 Dec (4)

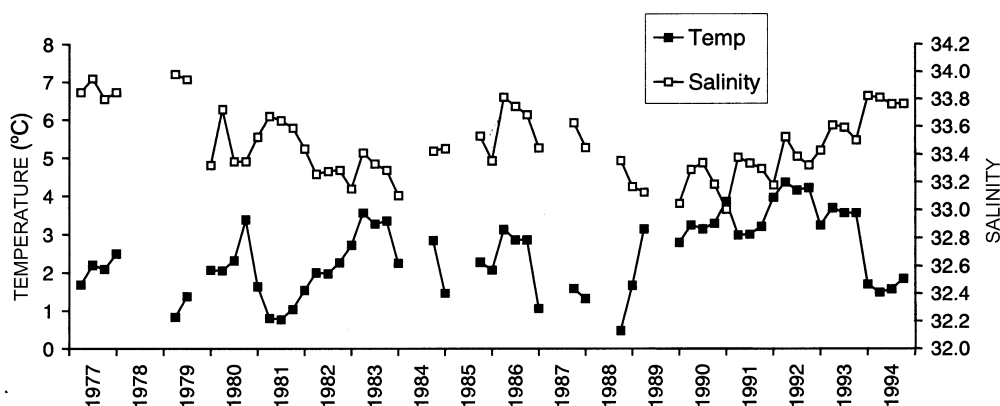


Fig. 2. Temperature and salinity at 175 m at Svartnes, Balsfjord from 1977 to 1994. Connecting lines have not been drawn at intervals in excess of 4 months between measurements.

RESULTS

HYDROGRAPHY AND BOTTOM SEDIMENTS

The temperature of the deep basin water (170 to 180 m) varied from 0.5 °C to 4.5 °C during the study (Fig. 2). The water was particularly cold in 1978, 1981, 1987 and 1988, while there was a period of relatively higher temperatures from 1989 to 1993. In most years, the temperature rose from spring to autumn and dropped during winter. The increases and decreases in temperature were due to inflows of deep water and turbulent vertical mixing, respectively (Finne & Gade 1990). Salinity variations were mostly small, although salinity was lowest in the periods showing the highest temperatures.

The bottom sediment consists of olive-grey soft mud. The fine fraction (particles < 0.063 mm) represented about 95 % of the sediment's dry weight, with maxima for clay and coarse silt (Fig. 3). The TOC content was about 2 % and the C/N ratio was 7 to 10 (Table 2). The

figures did not appear to vary seasonally. The present results coincide with previous measurements of grain size and organic matter at the same location (Velvin 1981; Sargent & al. 1983).

FAUNAL COMPOSITION

In total, 125 species or species groups (taxa) and more than 37 000 specimens were recorded. The fauna was dominated by annelids which comprised 78 species and represented 97 % of the individuals (Table 3). Other groups were sparsely represented, but moderate numbers of crustaceans (20 species) and bivalves (11 species) were found. The oweniid polychaete *Myriochele oculata* was the most prominent and numerically dominant species (Table 4). Usually, the long, thin tubes would form a dense lattice in the sieves when the sediments were washed out. Other commonly found species were small polychaetes such as *Lumbrineris*

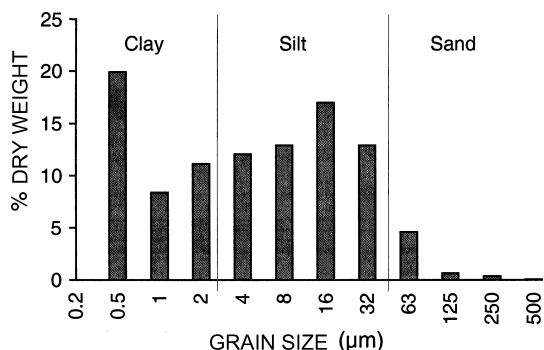


Fig. 3. Sediment grain size distribution. Median particle size in phi units (md phi) = 8.1, sorting (st phi) = 2.4.

Table 2. Organic content of surface sediments from Svartnes, Balsfjord. TOC = total organic carbon, TN = total nitrogen, C/N = carbon/nitrogen ratio. The two samples from January 1994 (1, 2) were taken from replicate grab hauls. The results from 1979-80 are from Sargent & al. (1983).

Date	TOC mg/g	TN mg/g	C/N
24 Jan 1994 (1)	24.1	2.5	9.6
24 Jan 1994 (2)	18.4	2.5	7.4
13 Sep 1994	20.3	2.8	7.3
13 Dec 1994	18.0	2.4	7.5
25 May 1979	23.6	2.4	9.8
21 Sep 1979	23.8	2.4	9.9
23 Nov 1979	23.8	3.3	7.2
17 Jan 1980	23.7	2.7	8.8

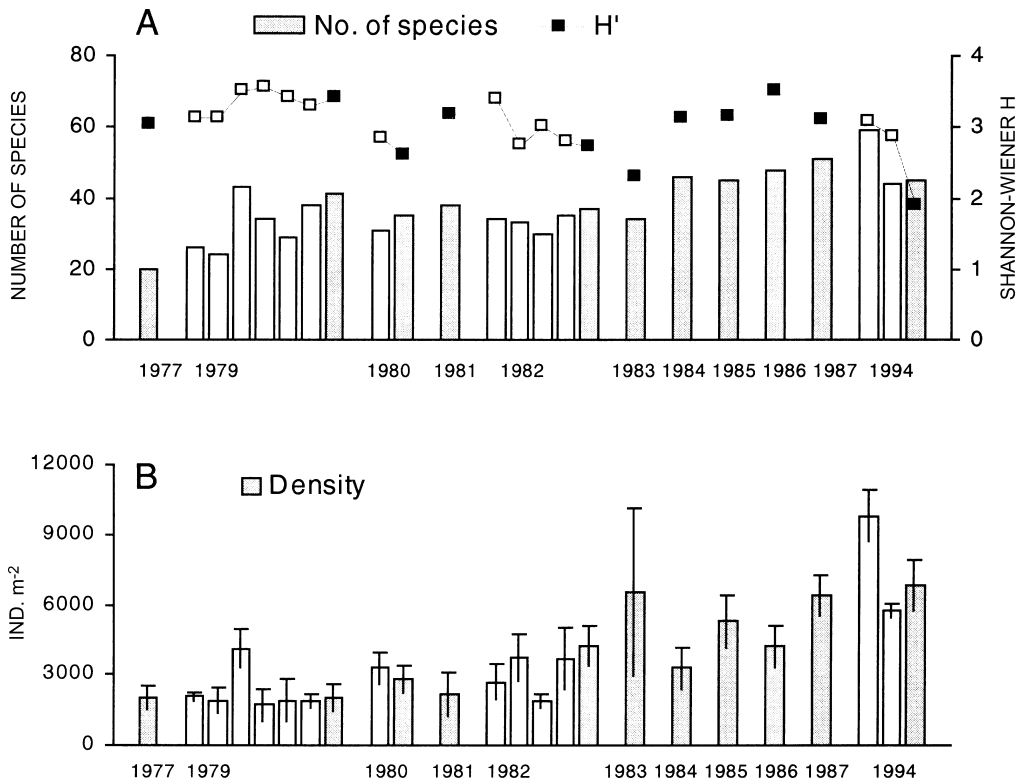


Fig. 4. Community statistics for soft-bottom macrofauna in Balsfjord 1977-1994. A. Number of species and Shannon-Wiener diversity (\log_2 base). B. Total densities (\pm standard error). Sampling for seasonal variations was performed in 1979 (Apr-Dec: 7 surveys), 1982 (Feb-Nov: 5 surveys) and 1994 (Jan-Dec: 3 surveys). Shaded columns/filled squares indicate autumn surveys used for assessing long-term patterns. The survey results from August 1978, March 1979 and March 1980 have been omitted due to too few grab samples.

mixochaeta, *Levinsenia gracilis*, *Prionospio cirrifera*, *Chaetozone setosa*, and *Heteromastus filiformis*, and the oligochaete *Tubificoides cuspidatus*. These species were present in all samples taken. Molluscs and crustaceans were far less common, and sometimes totally missing from individual replicate samples. The most frequently found molluscs were the caudofoveates, the protobranch bivalves *Nuculoma tenuis* and *Yoldiella lenticula* and the eulamellibranch *Thyasira*. The mud star *Ctenodiscus crispatus* was found regularly. This species is relatively large-sized, contributing substantially to the benthic biomass despite its comparatively low densities.

TRENDS IN SPECIES NUMBERS, DENSITIES AND DIVERSITIES

The number of species recorded per survey ranged from 20 to 59 (average: 37), and total densities ranged from 1713 to 9803 ind. m⁻² (average: 3914 ind. m⁻²) (Fig. 4). Species numbers and densities both increased during the study period. Species numbers increased moderately, but showed clearly higher values after 1983-84. The

Table 3. Number of identified taxa and percentage of total number of specimens of the major taxonomic groups at Svartnes, Balsfjord, from 1977 to 1994. The asterisk (*) indicates groups where species have not been identified.

Group	Number of taxa	% of specimens
Cnidaria	1	< 0.1
Nemertinea *	1	0.8
Nematoda *	1	< 0.1
Sipuncula	2	< 0.1
Annelida		
Polychaeta	78	83.2
Oligochaeta	1	14.0
Crustacea	20	0.2
Mollusca		
Caudofoveata *	1	0.5
Gastropoda	5	< 0.1
Bivalvia	11	1.0
Scaphopoda	1	< 0.1
Echinodermata		
Asteroidea	1	0.2
Ophiuroidea	2	< 0.1



densities increased substantially, rising from about 2000 ind. m⁻² before 1982 to more than 4000 ind. m⁻² after 1985. The trends were found statistically significant for both species numbers ($p < 0.05$) and densities ($p < 0.01$) in the mean square successive difference test using data from autumn (Oct.-Dec.) surveys (Fig. 4). No particular seasonal patterns were shown. During the three years

in which seasonal observations were made (1979, 1982, 1994), species numbers and densities varied unsystematically with peak values occurring at different times of the year. In some cases, minimum and maximum values occurred in consecutive sampling surveys. Species diversity showed no particular trends ($0.10 < p < 0.25$ for autumn surveys). Values of the Shannon-Wiener

Table 4. The most common taxa in soft-bottom samples from Balsfjord. The frequency of occurrence, mean density (ind. m⁻²) and min/max-densities refer to 27 surveys from December 1977 to December 1994. Abbr. = abbreviation of species names used in the principal component analysis plot. Feeding categories: c = carnivore, su = suspension feeder, sd = surface deposit feeder, ssd = subsurface deposit feeder. Classification into feeding categories is based on Fauchald & Jumars (1979), Barnes (1980), Shick & al. (1981), Josefson (1986), Tzetlin (1994), and Holte (1998).

	Abbr.	Feeding category	Frequency %	Mean dens. Ind. m ⁻²	Min/max dens. Ind. m ⁻²
NEMERTINEA ind.	Nemertin	c	93	31	0-75
POLYCHAETA					
<i>Harmothoe sarsi</i> (Kinberg)	-	c	41	2	0-13
<i>Eteone</i> cf. <i>longa</i> (Fabricius)	Eteo lon	c	93	14	0-30
<i>Nephtys ciliata</i> (O.F. Müller)	Neph cil	c	100	34	8-90
<i>Lumbrineris mixochaeta</i> Oug	Lumb mix	c	100	220	100-515
<i>Scoloplos armiger</i> (O.F. Müller)	-	ssd	63	6	0-85
<i>Leitoscoloplos mammosus</i> Mackie	-	ssd	48	4	0-35
<i>Aricidea</i> cf. <i>suecica</i> Eliason	-	sd/ssd	48	3	0-23
<i>Levinsonia gracilis</i> (Tauber)	Levi gra	sd/ssd	100	342	40-1020
<i>Paraonella</i> sp.	-	sd/ssd	56	3	0-13
<i>Apistobranchius tullbergi</i> (Théel)	-	sd	78	22	0-123
<i>Prionospio cirrifer</i> Wirén	Prio cir	sd/ssd	100	157	30-395
<i>Spiophanes kroeyeri</i> Grube	-	sd	78	14	0-68
<i>Chaetozone setosa</i> Malmgren	Chae set	sd	100	213	73-990
<i>Cossura longocirrata</i> Webster & Benedict	Coss lon	sd	93	44	0-437
<i>Heteromastus filiformis</i> (Claparède)	Hete fil	ssd	100	117	38-230
<i>Maldane sarsi</i> Malmgren	Mald sar	ssd	89	184	0-2283
<i>Praxillella gracilis</i> (M. Sars)	-	ssd	74	6	0-18
<i>Rhodine gracilior</i> Tauber	-	ssd	48	4	0-18
<i>Microclymene/Praxillella</i> spp.	Micr/Pra	ssd	81	36	0-155
<i>Myriochele heeri</i> Malmgren	-	ssd	74	117	0-1245
<i>Myriochele oculata</i> Zachs	Myri ocu	sd/ssd	100	1573	260-4885
<i>Pectinaria hyperborea</i> (Malmgren)	Pect hyp	ssd	89	16	0-80
<i>Sabellides borealis</i> M. Sars	-	sd	63	8	0-40
<i>Artacama proboscidea</i> Malmgren	Arta pro	sd/ssd	85	16	0-78
<i>Lanassa venusta</i> (Malm)	Lana ven	sd	85	7	0-18
<i>Laphania boeckii</i> Malmgren	-	sd	56	11	0-120
<i>Proclea malmgreni</i> (Ssolowiew)	-	sd	63	10	0-80
<i>Terebellides stroemi</i> M. Sars	Tere str	sd	93	33	0-135
<i>Chone</i> sp.	-	su	78	26	0-180
<i>Euchone papillosa</i> (M. Sars)	-	su	78	11	0-45
OLIGOCHAETA					
<i>Tubificoides cuspidatus</i> Baker	Tubi cus	ssd	100	528	5-1210
MOLLUSCA					
Caudofoveata ind.	Caudofov	c	96	20	0-80
<i>Nuculoma tenuis</i> (Montagu)	-	ssd	78	7	0-55
<i>Yoldiella lenticula</i> (Møller)	-	ssd	78	15	0-88
<i>Thyasira</i> spp.	-	su/ssd	70	15	0-115
ECHINODERMATA					
<i>Ctenodiscus crispatus</i> (Retzius)	Cten cri	sd/ssd	89	8	0-20

index (H') ranged from 1.89 (December 1994), which was an exceptionally low value, to 3.55 (July 1979). Most values were in the interval 2.7 to 3.4.

COMMUNITY VARIATION AND SAMPLE REPLICABILITY

The species composition was basically the same throughout the study period. Eight species were collected in all surveys and 19 species were found in more than 80 % of the samples (Table 4). These species represented 93 % of the total number of individuals. There was a high degree of faunal similarity among the samples. This was reflected in the correspondence analysis for individual samples, in which the inertias (eigenvalues) extracted on axes (0.16-0.04) and the total inertia (0.74) all were very low (Table 5). Usually, in CA axis values (eigenvalues) of 0.3 to 0.5 are taken as indicative of good separation of species or samples (ter Braak & Verdonschot 1995). The breakdown of the total inertia in successive CAs showed that about half of the variance (0.36) could be attributed to differences among surveys (Table 5). The rest of the inertia (0.38) is attributable to differences between replicate samples within surveys, representing spatial dispersion patterns. The relationship between the variance components is also reflected in the plot of the analysis, where the spread among sample replicates is generally of the same magnitude as the distance between sampling dates (Fig. 5). The inertia among surveys may further be divided in a component for years (0.23) and a component within years to encompass seasonal changes (0.13). Recalculated as percentages, the breakdown indicates that the replicate samples accounted for 51 % of the variation in the data set, while differences between the years accounted for 32 %, and variation within years was not more than 17 %. The difference between years appears to coincide with the location of the samples in the plot, for instance the samples from 1977, 1985-87 and 1994, which were fairly well separated (Fig. 5).

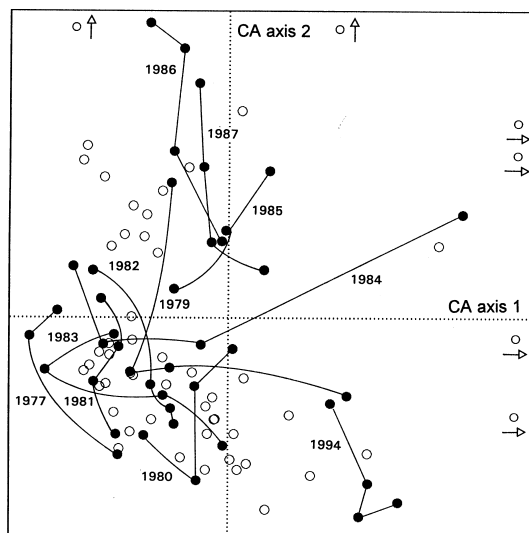


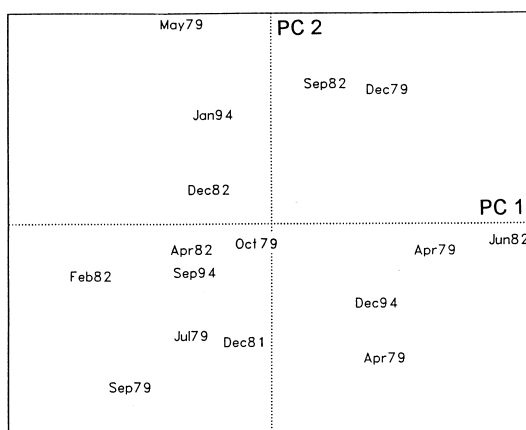
Fig. 5. Correspondence analysis (CA) ordination of individual soft-bottom macrofaunal samples from Balsfjord (95 samples). To illustrate the sampling variation, connecting lines have been drawn between replicate samples that belong together. One survey per year, taken during autumn (October-December), is depicted. Connecting lines between samples for other surveys, showing similar patterns, have been omitted for clarity.

TEMPORAL PATTERNS

During the course of the study there were moderate, but distinct changes for the most important species. In the PCA on pooled data for surveys, the first axis (41 % of the variation) contrasted the earliest (1977 to 79) and the latest (1994) samples with the years arranged approximately in sequence (Fig. 6A). This pattern indicates that the changes took place fairly gradually. The second axis (17 %) largely distinguished surveys within years (e.g. 1979, 1982), but did not reveal any particu-

Table 5. Summary of the main results of correspondence analyses (CA) on macrofauna data from Balsfjord: Inertia and percentage of explained variance for the first four axes. A. individual grab samples (95), B. sampling surveys (27), C. summarised data for years (12).

		Axis				Total
		1	2	3	4	
A. All samples	Inertia	0.16	0.07	0.06	0.04	0.74
	Expl. variance, %	22.0	9.0	7.5	5.2	
B. Surveys	Inertia	0.11	0.05	0.04	0.03	0.36
	Expl. variance, %	31.6	12.7	10.1	7.1	
C. Years	Inertia	0.08	0.05	0.03	0.02	0.23
	Expl. variance, %	32.2	19.7	12.0	10.2	



and did not form recognisable patterns (Fig. 7). However, most summer and early autumn samples (May to September) were located distally on the axes, possibly indicating that faunal variations were larger during summer than in autumn and winter periods.

The species community was dominated by sediment-ingesting organisms (Table 4). About 50 % of the total number of the species may be classified as surface or subsurface deposit feeders, and they constituted about 90 % (83-96 per survey) of the specimens in the community (Fig. 8). Carnivores accounted for about 10 % (4-14) of the specimens, while suspension feeders represented a small fraction only. Trophic composition varied little throughout the study, although the relative representation of carnivores decreased somewhat and surface deposit feeders tended to increase from 1983 to 1994. Scavengers and omnivores, such as motile crustaceans, were also present in the samples, but were not among the 40 most common species, and represented less than 1 % of the specimens.

The soft bottom in the deep basin of Balsfjord was inhabited by a rather homogeneous species assemblage characterised by small, sediment-ingesting forms. Numerically, the annelids dominated strongly, while ma-

The PCA carried out specifically to search for seasonal patterns did not reveal seasonal trends. The sampling dates were actually scattered around in the plot

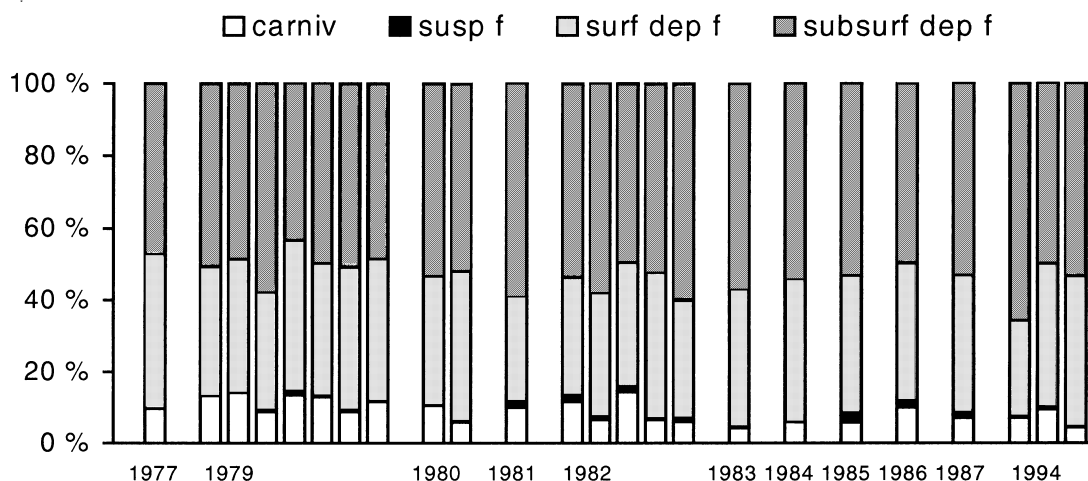


Fig. 8. The relative abundances of the main feeding categories (carnivores, suspension feeders, surface deposit feeders, subsurface deposit feeders) in the soft-bottom macrofauna in Balsfjord. The species classified into two feeding categories (cf. Table 4) were represented by 50 % of the specimens in each category.

major taxonomic groups such as molluscs, crustaceans and echinoderms were of minor importance and were not represented among the ten most abundant species. This rather undiversified species assemblage seems to differ in a number of respects from species assemblages in outer fjord areas and coastal waters, which are generally much more varied in terms of composition as well as functional attributes (cf. Holte & Oug 1996; Larsen 1997; Oug 1998a). However, similar annelid-dominated species assemblages have been reported from the deep basins of silled fjords elsewhere in northern Norway (Rombakfjord, 113 m; Kvænangfjord, 108 m) (Larsen 1997). Characteristically, *Myriochele oculata* dominates in all of these fjords. These species assemblages may represent a basic “fjord basin community” in northern silled fjords. Larsen (1997) drew particular attention to the reduction of echinoderms in the fjords. He also showed that faunal diversity was lower there than in open coastal areas, demonstrating, for instance, that the values of the Shannon-Wiener index (\log_2 base) decreased from between 4 and 6 in open coastal areas to 3 or lower in the fjord basins. Comparable faunal patterns have also been reported in glacier-influenced fjords elsewhere in northern Norway and in Svalbard (Holte 1998; Holte & Gulliksen 1998).

Obviously, the species assemblage reflects the ecological conditions in the deep basin of Balsfjord. Among the factors which generally influence the benthic fauna in fjords are the restriction of water exchange and circulation, and the proximity to land, which is of consequence for the input of nutrients and inorganic material

(Pearson 1980). Northern Norwegian fjords are characterised by being weakly stratified most of the year, and subject to turbulent mixing and frequent large-scale advective episodes (Eilertsen & al. 1981). In Balsfjord, most of the phytoplankton production appears to be mineralised in the water column or exported out of the fjord, while little reaches the fjord bottom. Lutter & al. (1989) estimated that the mean annual flux of phytoplankton carbon to the bottom was 0.9 g C m^{-2} per year, representing less than 1 % of the annual carbon production in the fjord. Euphausiid faecal pellets amounted to 2 to 3 g C m^{-2} , while the total amount of particulate carbon was estimated at 11 g C m^{-2} . However, Reigstad & Wassmann (1996) showed that advective episodes were particularly important for the vertical flux as they gave rise to resuspension of deposited detritus and introduced and removed specific zooplankton grazers. Specifically, they recorded pulses of sedimenting euphausiid faecal pellets and correlated them with advective episodes. Essentially, Reigstad & Wassmann (1996) interpreted the sedimentation in Balsfjord to consist of two components, a basic fraction with low seasonality, which exhibited only slightly increased fluxes of organic matter during the production season, and a variable fraction related to advection whose pulses depended on the content of nutrients and plankton in the advected water masses.

Consequently, the benthic fauna in the fjord basin seems to be dependent on a low, irregular supply of nutrient material of mostly low quality. Indeed, Sargent & al. (1983) found that the sedimentary detritus in the



Svartnes basin mostly consisted of refractive and partly decayed material. Micro-organisms seem to play a significant role in the mineralisation of the detritus, suggesting that a large proportion of the nutrients available to the benthic fauna may be derived from micro-organisms. This supposition has been substantiated by studies of the mud star *Ctenodiscus crispatus*, which accumulated fatty acids indicative of microbial input (Sargent & al. 1983; Hopkins & al. 1989). It is most likely that the macrobenthic organisms interact with micro-organisms in the benthic trophic pathways. Sub-surface deposit feeders, such as *Maldane sarsi*, *Heteromastus filiformis* and *Pectinaria hyperborea*, constitute an important component of the fauna and presumably play a significant role by transporting material from deep sediment layers to the sediment surface. Sub-surface deposit feeders, as for instance *H. filiformis*, may also enrich carbon material during feeding (Neira & Höpner 1994). Holte (1998) suggested that sub-surface feeders may be particularly important for the benthic trophic dynamics in nutrient-poor environments as they reintroduce buried carbon into the nutrient cycle.

No particular seasonal patterns were observed in the benthic community. The lack of seasonality is consistent with both the fairly stable physical conditions and the seemingly irregular nutrient input in the fjord basin. Supposedly, the nutrient pulses may be smoothed out on a year-round basis and actually represent a rather stable food resource for the benthos. Sargent & al. (1983) observed negligible seasonal variations in organic components in the sediment. Further, the activity of the micro-organisms may be assumed to be approximately constant year-round because of the low ambient temperatures (cf. Syvitski & al. 1987). However, a number of species reproduce seasonally and release planktonic larvae during spring and summer in Balsfjord (Falk-Petersen 1982a). Larvae are therefore available to colonise the community seasonally, but the settlement and initial growth of the larvae on the bottom is not recorded as most young recruits pass through the sieves (1 mm) used. In *Pectinaria hyperborea* and *Lumbrineris mixochaeta*, maturing gametes have been observed during winter (Velvin 1981; Oug 1998b). There is at least some periodicity in the physical factors in the fjord basin, which may control the reproductive processes. Vertical convection and the advective inflow of deep water during winter and spring represent regular phenomena which may be of importance, causing minor, but fairly consistent, yearly decreases and increases in temperature and salinity. Rather small seasonal changes have been found in the benthic communities in fjords in other areas. In Scottish sea lochs, Pearson & al. (1982) observed moderate changes with

respect to numerical abundance, while in the Oslo Fjord, Valderhaug & Gray (1984) reported a stable community in a relatively shallow area with little variation in the physical environment.

The gradual increase in densities which appeared to commence in 1982-83, suggests that factors influencing the benthic community changed during the course of the study. It is reasonable to consider the changes in relation to the nutrient dynamics in the fjord. Various studies have attributed benthic faunal increases to nutrient enrichment (e.g. Josefson 1987; Rachor 1990), and correlations between phytoplankton and zooplankton abundances and macrofaunal abundances have been demonstrated in long-term data from the Skagerrak and British coastal waters (Austen & al. 1991; Buchanan 1993; Frid & al. 1996). In Balsfjord there is not much to indicate that there has been any general nutrient enrichment in the fjord ecosystem. As far as has been observed, phytoplankton production has maintained the same magnitude throughout the study, although no regular measurements have been conducted (C.H. von Quillfeldt, pers. commn). At higher trophic levels in the pelagic system, however, changes occurred which may possibly have influenced the flux of material to the bottom. In particular, the euphausiids, which formed dense sound-scattering layers in the late 1970s and early 1980s (Hopkins & al. 1978, 1989), have varied in abundance, and the local capelin stock has virtually disappeared (E. Nilssen, pers. commn). Consequently, the flow of material and energy through the pelagic systems may have taken alternative routes, and the input to the bottom may have increased, providing more food to the benthic fauna. Advection may be a key factor, and Reigstad & Wassmann (1996) showed that the vertical material flux was larger in 1992 than in 1982. However, the complex interactions in the fjord between advection, plankton stocks and particle dynamics are not well enough understood to estimate variations in the input to the benthos.

Another possibility is that the benthic fauna was adversely affected by the prawn trawling until the fishery was discontinued in 1983. Prawn trawling represents a physical disturbance as the trawl ploughs through the substrate and resuspends fine mineral particles which subsequently settle on the sediment surface. Recent studies have shown that the responses of smaller invertebrates to trawling disturbance vary depending on habitat type and intensity of fishing, but generally small opportunistic species tend to increase in disturbed areas (Lindeboom & de Groot 1998). In a study in a sheltered Scottish sea loch, the number of species and individuals increased and the diversity decreased following trawling disturbance (Lindeboom & de Groot 1998; Tuck & al. 1998). This response is in contrast with the



faunal changes observed in Balsfjord during and after the period of prawn trawling. Further, fragile bodied species, such as molluscs and brittle stars, which would be most vulnerable to trawling disturbance did not increase after the termination of the trawling. Evidence therefore does not support the supposition that prawn trawling was important for the faunal changes.

Few large predators exploit the soft bottom fauna. In Balsfjord, cod *Gadus morhua* L. and long-rough dab *Hippoglossoides platessoides* (Fabr.) are the only important demersal fish species. Cod mainly feed on prawns, capelin and euphausiids, although they take a small percentage of *Nephlys*, while dab select benthic epifauna and hyperbenthic crustaceans (Klemetsen 1982, 1993). However, dab are not common in the Svartnes Basin. The prawns seem to depend on pelagic organisms for food and, from a trophical point of view, do not belong to the benthic systems (Hopkins & al. 1989, 1993). Presumably, therefore, the soft-bottom faunal changes were not induced by predator feeding activities.

It appears that the strongly annelid-dominated species assemblages in the basins of Balsfjord and other silled northern Norwegian fjords (cf. Larsen 1997) are typical of these fjords, and may differ from bottom communities in other fjords, especially in boreal waters. Syvitski & al. (1987) assumed that fjord basin environments in general would support biologically-accommodated species communities characterised by large long-lived organisms, considering that the fjord-floor environment is one of physical homogeneity in space and time. Such communities have, for instance, been ob-

served in Scottish, Canadian and Alaskan fjords. They noticed, however, that relatively little is known about subtidal infaunal communities in the majority of fjord environments. Reigstad & Wassmann (1996) pointed out that the fjords in northern Norway display a number of characteristics which distinguish them from boreal and other high-latitude fjords in terms of physical stability as well as ecosystem dynamics. For instance, the fjords are weakly stratified and Arctic with respect to the light regime, yet strongly influenced by Atlantic water masses and generally ice-free during winter. Advection, in particular, is significant for the vertical fluxes by giving rise to extensive particle resuspension and through the import and export of specific plankton stocks in the fjords. In many respects the species assemblages are similar to bottom communities in glacier-influenced fjords, which are subjected to seasonal sedimentation of finely particulated inorganic material (Holte & Gulliksen 1998). In these fjords, small polychaetes and to a certain extent small deposit-feeding bivalves dominate the soft-bottom communities.

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