Macrobenthic biomass, productivity ($P/\overline{B}$) and production in a high-latitude ecosystem, North Norway

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ABSTRACT: Macrobenthic invertebrate biomass, productivity ($P/\overline{B}$ ratio) and production were estimated for a high-latitude fjord ecosystem, Sørfjord, North Norway. A model including individual weight, temperature, depth, taxonomical group, tidal-zone position, faunal category, motility and habitat was used to estimate $P/\overline{B}$ ratios, and production was calculated by multiplying $P/\overline{B}$ by biomass. Average biomass, production, abundance and $P/\overline{B}$ were 307 g wet weight (ww) m^{-2} (SE = 84, SD = 595, n = 50), 89 g ww m^{-2} yr^{-1} (SE = 16, SD = 112, n = 50), 1912 N m^{-2} (SE = 204, SD = 1442, n = 50) and 0.29 yr^{-1}, respectively. Converted to energy, average biomass was 441 kJ m^{-2} and production 185 kJ m^{-2} yr^{-1}. Horizontal and vertical trends were only detected for abundance, but a Monte Carlo test confirmed that subareas, depth and sediments explained a significant part of the variance in the community composition. Polychaeta was the most abundant and productive group, while large mussels (*Arctica islandica* and *Musculus niger*) and detrivorous asteroids (*Ctenodiscus crispatus*) dominated biomass. Even if biomass should always be measured for the area in question, $P/\overline{B}$ ratios from this study are considered reasonable for other North Norwegian fjords and coastal areas with similar conditions when an approximate measure of production is needed. In Sørfjord, the macrobenthic invertebrate production was much higher than the amount eaten by fish, and predatory benthos are probably more important consumers of benthic invertebrates.

KEY WORDS: Macrobenthos · Macrobenthic invertebrates · Production · Productivity · $P/\overline{B}$ ratio · Biomass · Abundance · High-latitude systems

INTRODUCTION

Modern fishery management relies on ecosystem models where all the important biological components of the systems are considered (Christensen 1995, Bradford-Grieve et al. 2003, Harvey et al. 2003, Rybarczyk et al. 2003). Petersen & Jensen (1911) recognised the importance of benthic invertebrates in the diet of demersal fish and were among the first to quantify benthos and estimate its potential as fish food. Small benthic invertebrates are also eaten by larger benthic invertebrates (Petersen & Jensen 1911), mammals (Hjelset et al. 1999) and birds (Johansen et al. 1999), and are important in the remineralisation and redistribution of sedimenting organic matter (Wassmann 1998). Consequently, benthic invertebrates represent a link, both directly and indirectly, in the energy transfer from primary producers to higher trophic levels. In addition, benthic living organisms are becoming increasingly popular in the human diet. Good quality and high market price make them favoured species for fisheries and aquaculture.

Predictive empirical models and regressions have been constructed to estimate secondary production of benthic invertebrates from easily obtained parameters and variables (e.g. Zaika 1970, Banse & Mosher 1980, Tumbiolo & Downing 1994, Brey 1999, 2004). Time and money are important constraints for most studies, and when whole communities are studied, the application of such models is helpful. Cusson & Bourget (2005) have evaluated some of the models and concluded that they successfully predicted the observed production

values. Ideally, it is preferable to have separate information on all species in a system, but considering the costs of obtaining data and because most ecosystem models use composite groups, approximate estimates of larger taxonomical units are often an acceptable alternative.

The benthic communities of high-latitude systems are among the richest in the world, and despite harsh physical conditions, an abundant and diverse benthic fauna has been observed (McLusky & McIntyre 1988). Research on in- and epifaunal macroinvertebrates in these waters has traditionally focused on taxonomy and species diversity, and little effort has been made to assess the ecological significance of benthic invertebrates as producers and/or consumers. Due to this scarcity of data, existing ecosystem models of Norwegian fjords (Bax & Eliassen 1990, Salvanes et al. 1992) treat benthos in a simplified way, and data on biomass, mortality and production are borrowed from other regions where biotic and abiotic conditions can vary greatly from the area in question.

This study was carried out to estimate the productivity ($P/\bar{B}$ ratio) (yr^{-1}) and to give an approximate measure of the average production (m^{-2} yr^{-1}, and for the whole fjord yr^{-1}) of the benthic macroinvertebrate community in the high-latitude fjord Sørfjord, North Norway. Variable hydrographical conditions within the fjord were assumed to affect benthic structuring factors such as food availability and sediment surface and result in a horizontal and vertical response in benthic production. Brey's (1999) model (Version 2-00) was used to estimate $P/\bar{B}$ ratios of composite taxonomical groups. Versions of this model have also been used by e.g. Brey & Gerdes (1998, 1999) and Cartes et al. (2002). Cusson & Bourget (2005) concluded that a later version of Brey's model (Version 4-04) (Brey 2004) was considered the best alternative of a number of production models tested.

Benthos is important in the diet of demersal fish (Kanapathippillai et al. 1994, Mikkola 1996) and birds (Johansen et al. 1999) in Sørfjord. The results from the present study are intended to be included in a trophic model for the Sørfjord system. In addition, the productivity ratios are valuable for assessing the role of benthos and modelling of other high-latitude ecosystems. With little biomass, production and productivity data available from other high-latitude systems (Cusson & Bourget 2005), the results are evaluated and compared with data from other parts of the world.

MATERIALS AND METHODS

Study area. Sørfjord is located at 69° 40′ N, 19° 40′ E, 30 km east of the city of Tromsø, North Norway (Fig. 1). It is approximately 27 km long and 3 km wide, and has a total area of ca. 55.2 km^2. The bathymetry features 2 deep basins (Tarehola and Njosken), about 130 m deep, separated by a shallow (Skognes) of 50 m. A second shallow of ca. 50 m depth (Storura) is located at the head of the fjord (Fig. 1). A narrow and shallow sill, 300 m wide and 8 m deep, in the mouth of Sørfjord separates it from Ullsfjord (Fig. 1).

Tidal exchange, with warm and saline Atlantic water flowing in from Ullsfjord, creates a turbulent and well-mixed water column in Tarehola throughout the year (Sælen 1950). The inner subareas (Skognes, Njosken and Storura) are colder and less saline and a thermocline develops at approximately 50 m during summer/autumn (Sælen 1950). At the time of investigation (11 to 15 January 1999), bottom temperatures and salinities were 2.9 to 3.3°C and 33.4 to 33.7 PSU, respectively. During summer, bottom temperatures reach 9°C in Tarehola.
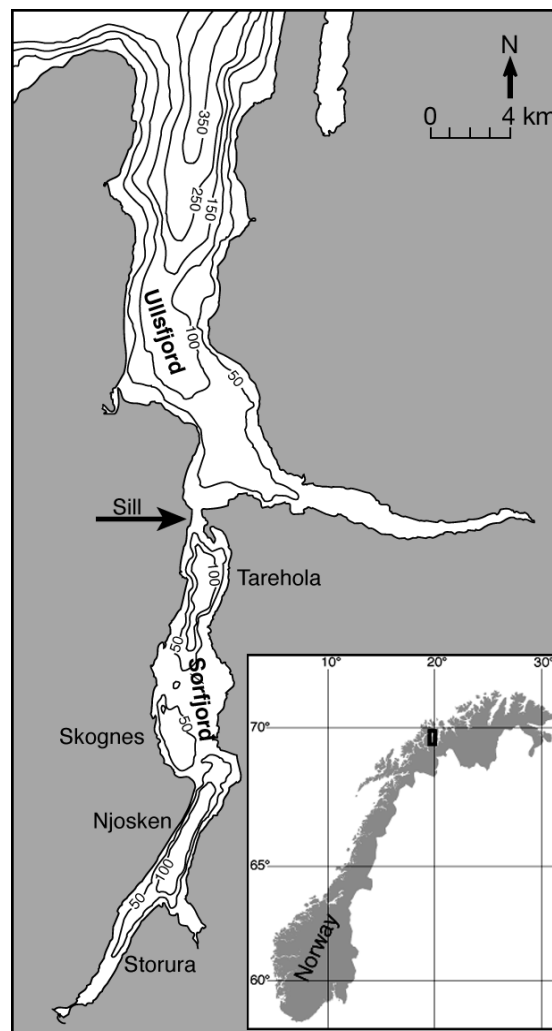

Fig. 1. Sørfjord and Ullsfjord, North Norway. Four subareas of Sørfjord indicated by names; location of sill separating fjords indicated by arrow. Depth contours (m) are shown

Field sampling. The objectives of this study are (1) detection of differences in macrobenthic mean abundance, biomass and production between defined subareas and depth intervals, delimited by the average depth of the summer pycnocline, within a fjord, and (2) estimation of fjord overall means for the above 3 variables. Sampling design had to meet the spatial scale requirements specified by the above objectives, subject to the constraint of a maximum number of 50 grab samples set by sampling and processing costs. A stratified random design of 50 stations with 1 grab sample collected per station, distributed over the 4 subareas Tarehola (n = 14), Skognes (n = 12), Njosken (n = 12) and Storura (n = 12) and the 2 depth intervals 0 to 50 m (n = 26) and >50 m (n = 24) was chosen (Fig. 1). Given the stated objectives and constraints, the sampling design adopted in this study is considered to be a more efficient strategy than comparing a few stations with several replicates. This sampling design provides a better estimate of means, given a constant sum of samples (Bogstad et al. 1995). The shallowest station was located at 18 m, the deepest at 128 m. A 0.1 m^2 van Veen grab was used. Grab samples were accepted if at least ¾ filled, closed and with an undisturbed surface. The complete grab content was processed. Standard error to mean ratios of 27, 18 and 11 % for wet weight biomass, production and abundance, respectively, indicated acceptable precision of the mean estimate.

Sediments were visually inspected and classified into the following categories: (1) clay, (2) silt, (3) sand, (4) gravel, (5) stone, or (6) a percentage mixture. Sediments were classified to obtain a general idea of the sediment structure in the fjord and are discussed in a broad sense. Samples were sieved through 1 mm mesh sieves and the material (macrofauna) was fixed in 6 % hexamethyl buffered formaldehyde or frozen (large individuals).

Laboratory work. All samples were processed in the laboratory within 1 yr. Animals were classified into 28 taxonomical sorting groups of different levels (phyla, classes, orders, families, genera or species) (Table 1) to which analyses were applied. The mussels *Arctica islandica* (ocean quahog) and *Musculus niger* (black mussel), the mud star *Ctenodiscus crispatus*, the whelk *Buccinum* sp. and the spider crab *Hyas coarctatus* were identified to species/genus level because of their high individual weights. Species included in most other sorting groups have relatively similar body size and ecology. For each sorting group, wet weight (shells included) was measured and individuals were counted. Individuals were blotted dry for a few seconds before weighing. All organic material was included in the weight. A separate category was defined

Table 1. Statistical groups and sorting groups. Animals were classified into 28 sorting groups, and sorting groups were compiled into 10 statistical groups prior to statistical analysis. Polychaeta, the mollusc species *Arctica islandica* and *Musculus niger* and the echinoderm *Ctenodiscus crispatus* were treated as separate sorting and statistical groups. Abbreviations given in parentheses correspond to abbreviations used in Fig. 3b

Statistical group	Sorting groups
Polychaeta	Polychaeta (Pol)
A. islandica	*A. islandica* (Ais)
M. niger	*M. niger* (Mni)
C. crispatus	*C. crispatus* (Ccr)
Crustacea	Cirripedia (Cir)
	Mysida (Mys)
	Cumacea (Cum)
	Amphipoda (Amp)
	Euphausiacida (Eup)
	Caridea (Car)
	Anomura (Ano)
	Brachyura (Bra)
	Hyas coarctatus (Hco)
Mollusca	Polyplacophora (Pop)
	Bivalvia (Biv)
	Scaphopoda (Sca)
	Gastropoda (Gas)
	Buccinum sp. (Buc)
Echinodermata	Asteroida (Ast)
	Ophiuroidea (Oph)
	Echinoida (Ech)
Rest	Actinaria (Act)
	Priapulidae (Pri)
	Hirudinea (Hir)
	Pycnogonida (Pyc)
	Brachiopoda (Bpo)
	Ascidiacea (Asc)
	Unidentified (Uni)
Polychaeta excluded	Total excluding Polychaeta
Total	All groups

for unidentified organic material (e.g. animal parts/segments), constituting 0.4 % of total wet weight biomass. Average individual weight for the respective sorting groups was computed by dividing their biomass with their abundance for each station.

Data analysis. *Estimations of productivity and production:* A yearly somatic $P/\bar{B}$, given with a 95 % confidence interval, was estimated using a model developed by Brey (1999), later modified and made available in an Excel worksheet (Version 2-00). The model is given by the equation:

$$\log P/\bar{B} = 8.256 - 2.226\log M - 2432.055(1/T + 273) + 0.239(1/D) + 0.241 D_{subt} + 0.203 D_{inf} + 0.242 D_{moti} - 0.287 D_{moll} - 0.203 D_{poly} - 0.128 D_{crust} - 0.457 D_{echi} - 0.116 D_{lake} + 562.218\log M (1/T)$$

where *M* is average body mass (kJ), *T* is temperature (°C) and *D* is depth (m). Dummy variables are set to 0 (no) or 1 (yes) for the categories (1) subtidal species (D_{subt}), (2) infauna (D_{inf}), (3) motile epifauna (D_{moti}), (4) Mollusca (D_{moll}), (5) Polychaeta (D_{poly}), (6) Crustacea (D_{crust}), (7) Echinodermata (D_{echi}) and (8) lake (D_{lake}). For other taxa dummies are also set to 1 for Polychaeta.

The model describes relations between given parameters as observed in nature. Empirical data derived from several studies from different parts of the world is used as its basis, and the model is continuously updated as new data become available. The model depends on the negative exponential relation of metabolic rate to biomass, and the parameters are logarithmically transformed to achieve linear relations required for linear regression models. Separate $P/\bar{B}$ ratios were computed for each sorting group at each station and production was estimated by multiplying $P/\bar{B}$ by wet weight biomass or kJ for the respective group at that station. Since production was computed from $P/\bar{B}$ ratios, repeated sampling was not needed.

Wet weight biomass and average individual weights were converted to kJ through ash-free dry weight using weight conversion factors derived from Rumohr et al. (1987), Brey et al. (1988) and Ricciardi & Bourget (1998). When factors were not available for the respective sorting groups, factors from species/genera/families thought to dominate were used. Unidentified material was not included in productivity and production estimates because of uncertainties concerning taxonomical position and conversion factors.

To (1) meet the criteria stated of obtaining overall means for the fjord, (2) make the discussion clearer, and (3) for strictly statistical purposes the 28 sorting groups were further compiled into 10 statistical groups (Table 1). Average production for the different statistical groups in the whole fjord, subareas and depth ranges was estimated by dividing the sum of production by the number of stations. Average $P/\bar{B}$ ratios for the different statistical groups and for the total benthic community were estimated from the sum of production divided by the sum of biomass of the respective groups. The average benthic community production was estimated as the sum of production of all the sorting groups divided by the number of stations. Overall production of the benthic community in Sørfjord was estimated by multiplying average production by the total fjord area.

Biomass, production and abundance in relation to the abiotic environment: Along with the total material, the most abundant or interesting statistical groups were tested for differences in horizontal (subarea) and vertical (depth interval) distribution. An analysis of covariance (ANCOVA), with depth as a co-variable, was used for testing differences between subareas and

a separate variance *t*-test was used for testing differences between depth intervals. Due to non-normality all tests were performed on $\log_{10}$-transformed data. Both the ANCOVA and the *t*-test are considered to be robust and to operate well even with heterogeneous variance, as long as n_i are equal or nearly equal.

Similarities of sorting groups and stations were expressed by an indirect correspondence analysis (CA), which provides a simultaneous ordination of taxonomical groups and stations along the axis. Canonical correspondence analysis (CCA), involving direct gradients, was applied to relate the biological patterns to the environmental variables. Environmental variables represented as vectors in the ordination plot were: (1) depth, (2) temperature and (3) salinity at the bottom. Sediment categories and subareas were treated as nominal environmental variables in the plots. A Monte Carlo permutation test selected environmental variables that significantly explained the patterns of the data. A comparison of the sum of eigenvalues of CA and CCA indicates the amount of variance explained by the environmental variables included. The tests were performed on square root-transformed data choosing the option of downweighting rare 'species' (sorting groups).

RESULTS

Average wet weight biomass, production and abundance for the macrobenthic community of Sørfjord were 307 g m^{-2} (SE = 84, SD = 595, n = 50), 89 g m^{-2} yr^{-1} (SE = 16, SD = 112, n = 50) and 1912 N m^{-2} (SE = 204, SD = 1442, n = 50), respectively (Fig. 2a,c,e). Converted to energy, average biomass was 441 kJ m^{-2} and average production 185 kJ m^{-2} yr^{-1}. The overall production was 4913 t ww yr^{-1} when the total area of Sørfjord was considered. By dividing the sum of wet weight production by the sum of wet weight biomass (not including unidentified material), an average community $P/\bar{B}$ ratio of 0.29 yr^{-1} was estimated for macrobenthic invertebrates in Sørfjord; the corresponding ratio based on kJ data was 0.42 yr^{-1}.

Estimated average Sørfjord $P/\bar{B}$ ratios for the statistical groups Polychaeta, Crustacea, Mollusca and Echinodermata were 0.75, 0.45, 0.35 and 0.37 yr^{-1}, respectively. Because of high individual weights, *Arctica islandica*, *Musculus niger*, and *Ctenodiscus crispatus* contributed largely to biomass (Fig. 2a) in spite of low abundance (Fig. 2e). Low estimated $P/\bar{B}$ ratios (*A. islandica*: 0.18 yr^{-1}, *M. niger*: 0.25 yr^{-1} and *C. crispatus*: 0.16 yr^{-1}) resulted in a lower contribution to total production compared to biomass (Fig. 2a,c). Polychaeta was the only group present at all stations; it dominated abundance (Fig. 2e) and had the second

highest biomass (Fig. 2a). The combination of high $P/\bar{B}$ ratio and high biomass made Polychaeta the most productive group in Sørfjord (Fig. 2c).

When the subareas were compared, average abundance was significantly higher in Skognes than in Tarehola (Fig. 2e, Tables 2 & 3). The apparently higher

biomass and production in Skognes (Fig. 2a,c) were not confirmed by statistical tests. Abundance was, however, higher in Tarehola than in all other subareas when Polychaeta was eliminated (Fig. 2f, Tables 2 & 3). Average $P/\bar{B}$ ratios of the subareas varied moderately. $P/\bar{B}$ ratios in Tar ehola and Njosken (both 0.31 yr^{-1})
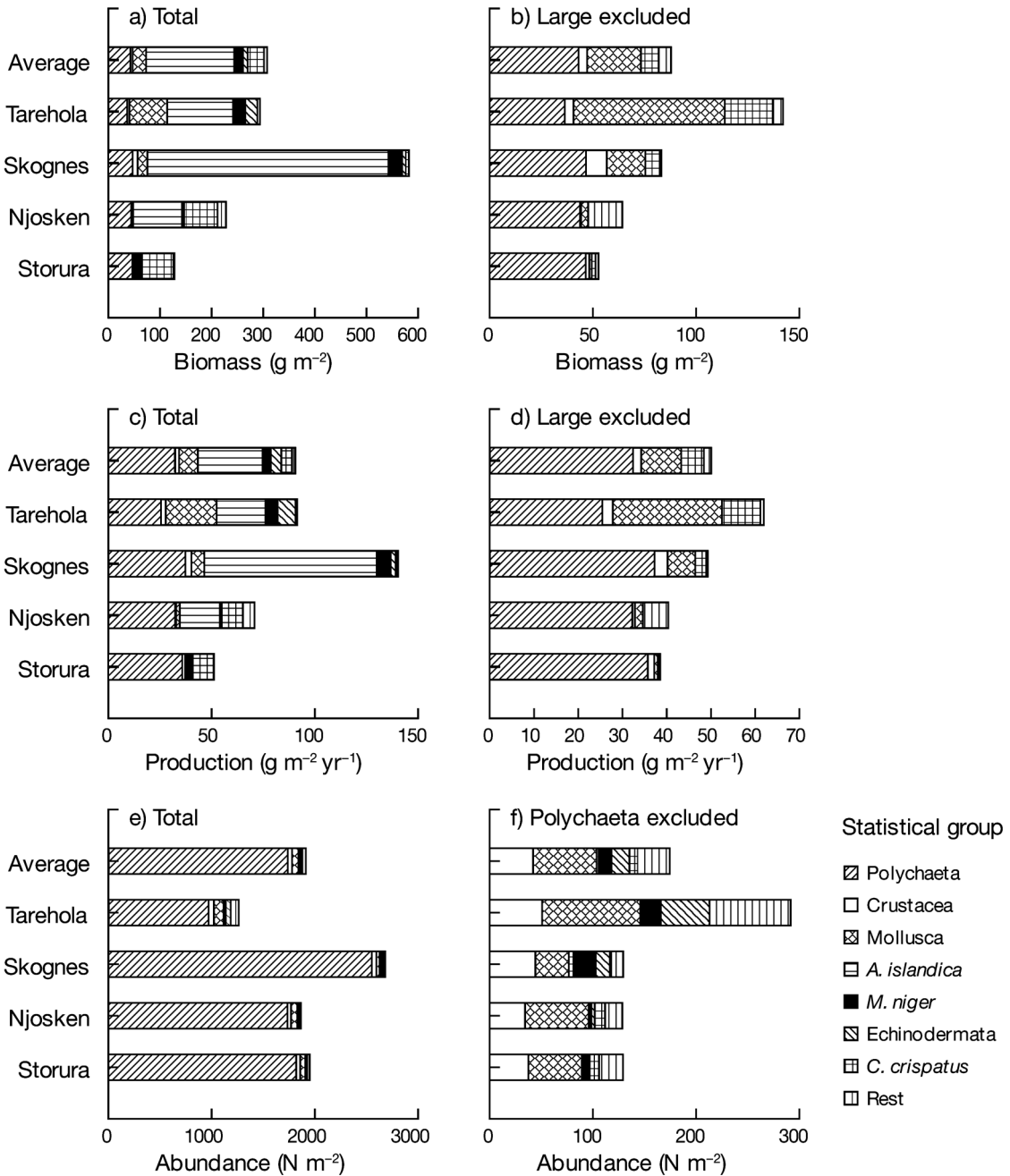

Fig. 2. Average benthic wet weight biomass (g m^{-2}), wet weight production (g m^{-2} yr^{-1}) and abundance (N m^{-2}), including the average contributions of the different statistical groups. Average for the whole Sørfjord and for the subareas Tarehola, Skognes, Njosken and Storura are shown. (a) Total biomass, (b) biomass with the 3 large species *Arctica islandica*, *Musculus niger* and *Ctenodiscus crispatus* excluded, (c) total production, (d) production with the 3 large species *A. islandica*, *M. niger* and *C. crispatus* excluded, (e) total abundance and (f) abundance with Polychaeta excluded

were close to the community average (0.29 yr^{-1}), Skognes had a lower $P/\bar{B}$ ratio (0.24 yr^{-1}) while the $P/\bar{B}$ ratio in Storura was higher (0.40 yr^{-1}).

Differences between stations from depths above and below 50 m were not evident for total benthic biomass, production or $P/\bar{B}$ ratios, but abundance was higher at deep stations ($t = 2.85$, df = 43.4, p = 0.007). The importance of depth on abundance was also shown by the ANCOVA test (Table 2). When Polychaeta was removed, no depth trend was shown in abundance. Abundance ($t = 3.13$, df = 40.1, p = 0.003), biomass ($t = 2.15$, df = 48.0, p = 0.037) and production ($t = 2.48$, df = 48.0, p = 0.017) of Polychaeta were all higher at stations deeper than 50 m compared to stations shallower than 50 m.

Correspondence analyses performed on biomass, production and abundance data showed relatively similar patterns; hence, only the results from the production data are given. Eigenvalues of 0.5 and 0.4 for the first 2 axes in the ordination plot (Fig. 3) reflect a relatively good separation of sorting groups. The first 2 axes accounted for 42% of the variance in sorting groups, and the environmental variables included explained 40% of the total variance. Subareas and sediments dominate the gradients in the first 2 axes (Fig. 3)

Table 2. ANCOVA test results of differences in means between subareas (Tarehola, Skognes, Njosken and Storura, df = 3.45) with depth (df = 1.45) treated as co-variable. The test was applied on log$_{10}$-transformed abundance data

	F	p
Total abundance		
Subarea	3.88	0.015
Depth	6.56	0.014
Abundance w/o Polychaeta		
Subarea	5.62	0.002
Depth	3.10	0.085

Table 3. Significant results (p-value) from Bonferroni post-hoc tests of differences between subareas (df = 45)

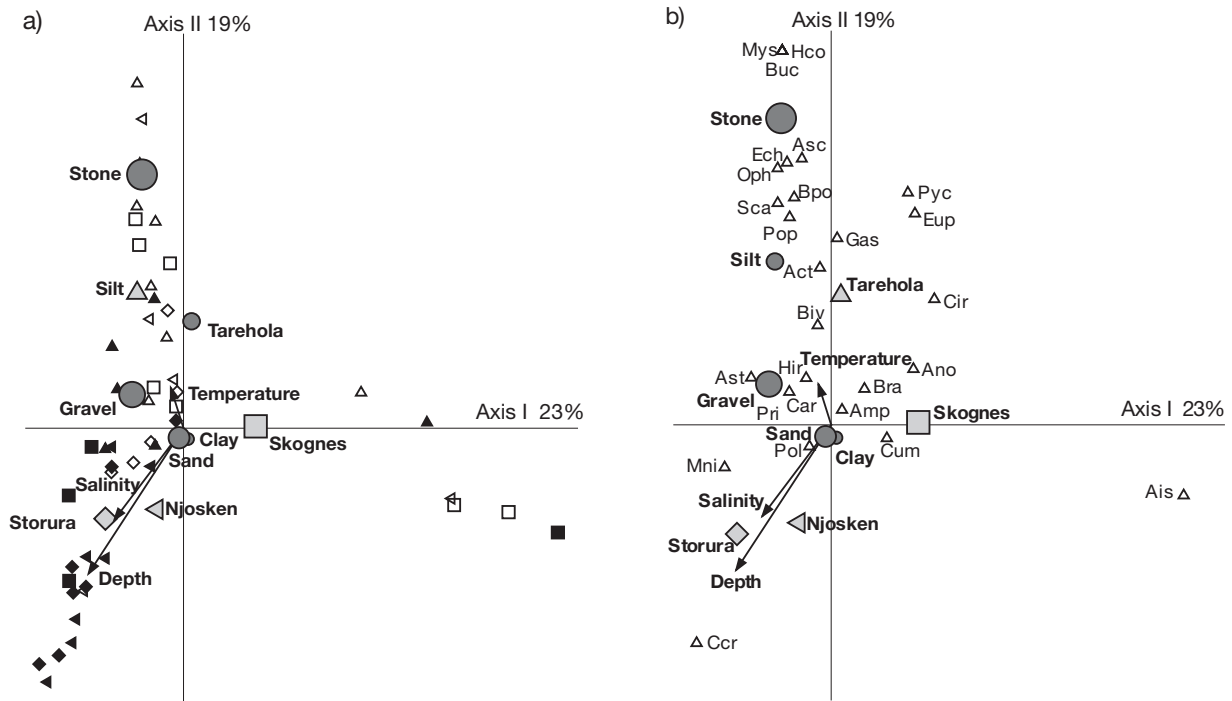| Subarea	p
Total abundance	
Tarehola – Skognes	0.019
Abundance w/o Polychaeta	
Tarehola – Skognes	0.024
Tarehola – Njosken	0.015
Tarehola – Storura	0.006

Fig. 3. Correspondence analysis (CA) (Axes I and II) of benthic production data describing their relationship with selected environmental variables. Arrows show direction and strength of depth, salinity and temperature. Subareas (Tarehola, Skognes, Njosken and Storura) and sediments (clay, silt, sand, gravel and stone) are shown as nominal variables. Ordinations of (a) stations and (b) sorting groups are displayed separately. Station symbols correspond with subarea symbols: open symbols for stations 0 to 50 m, filled symbols for stations >50 m. Abbreviations of sorting groups given in Table 1

and a forward selection and Monte Carlo permutation test (999 permutations) confirmed that Tarehola (F-value = 3.61, p = 0.002), Skognes (F-value = 3.38, p = 0.003), depth (F-value = 2.93, p = 0.003) and the occurrence of stone (F-value = 2.91, p = 0.032) and silt (F-value = 2.29, p = 0.019) all contributed significantly to the observed production pattern. Input of coarse sediments like stone and gravel are most abundant in Tarehola, while finer grained sediments dominate in Njosken and Storura (Fig. 3a). There is a tendency of a sediment depth gradient with a relatively homogenous clay substrate dominating at stations deeper than 50 m, while input of coarser sediments is more frequent at shallow stations (Fig. 3a). Typical coarse and hard-bottom taxa such as Polyplacophora, Ophiuroidea, Echinodermata, Pycnogonidae and Actinaria were positioned near Tarehola, following the dominance of coarser sediments (Fig. 3b). The highly abundant Polychaeta show weak correlations to all of the included environmental variables (Fig. 3b).

DISCUSSION

Evaluation of productivity and production estimates

Functional groups of organisms are used in most ecosystem models and, because of the constraints set by processing costs, such groups are also used in the productivity model in the present study. One should, however, be cautious and aware of the implications this may have for the estimated $P/\overline{B}$ ratios. $P/\overline{B}$ ratios are species specific (Banse & Mosher 1980), but variations in $P/\overline{B}$ ratios are often small between related species (McLusky & McIntyre 1988). For strictly mathematical reasons the logarithmic nature of the model underestimates $P/\overline{B}$ ratios for the different groups when species are combined in advance. However, most sorting groups in the present study consist of few closely related species of similar sizes and with comparable ecology and this is a factor of little importance. The exception is Polychaeta. In Balsfjord (69° 22′ N, 19° 07′ E), a neighbour fjord to Sørfjord, Polychaeta constituted 78 of 125 benthic species (Oug 2000). Species or family identifications, or an ecological categorisation into e.g. an errant and a sedentary group, would minimise the possible estimation error. Together with the use of winter temperatures rather than yearly averages and the exclusion of unidentified material, this points towards an underestimated production in this study. The precision of the weight conversion factors also influences the results, but the direction varies between groups. Calculations of wet weight production from somatic $P/\overline{B}$ ratios by multiplying this by wet weight biomass including shells overestimates produc-

tion, but still give an idea of the wet weight production. A higher average community $P/\overline{B}$ ratio based on the respective kJ data demonstrates the discrepancy of using wet weight vs. kJ since those individuals with the highest average body mass and thus the lowest $P/\overline{B}$ ratios have the highest percentage of inorganic matter as well. Providing the average biomass and production in kJ allows for more comparisons between this and later studies.

Although biotic variables defined for the respective taxonomical groups are the most important in explaining $P/\overline{B}$ ratios of benthic invertebrates, the ratios are also closely linked to environmental factors, mainly temperature and depth (Brey & Gerdes 1998, Cusson & Bourget 2005). The exponential relation between temperature and metabolism is reflected in both population (Tumbiolo & Downing 1994) and community (Brey & Clarke 1993) $P/\overline{B}$ ratios with lower ratios at low temperatures. The decrease in community production with depth (Brey & Gerdes 1998) is most likely explained by a decreased food input to the benthos with increasing water depth. Benthic biomass, production and productivity data from various regions of the world are compiled in Table 4. Making the general assumption that temperature and latitude are inversely related, the Sørfjord data fits the expectation of low $P/\overline{B}$ ratios at high latitudes (Cusson & Bourget 2005). One should, however, keep in mind that the generalised temperature–latitude relation is modified by physical factors such as depth, ocean circulation patterns, solar input and sea ice cover (e.g. Brey & Gerdes 1998, Cusson & Bourget 2005). Clarke (1991) suggests that limited food availability is the main cause for the low $P/\overline{B}$ ratios observed at high latitudes. In high latitudes, benthic food input is largely influenced by the match or mismatch between phytoplankton blooms and zooplankton abundance. In years of good match, the vertical export of biogenic matter to the seafloor is low, while a mismatch scenario is followed by a large-scale vertical export (Reigstad et al. 2000).

Assuming that $P/\overline{B}$ ratios at both the population and the community level varies only moderately given comparable environmental conditions, ratios from one area may be used in other areas with similar conditions. The extensive Norwegian coastline traverses a wide range of physical conditions, from the boreal North Sea to the arctic Barents Sea. A number of $P/\overline{B}$ ratios are estimated from North Sea areas (Table 4) and may be applicable to south Norwegian fjords (e.g. Salvanes et al. 1992), but, being ca. 2 to 17 times as high as the ratios calculated for Sørfjord, production in North Norwegian fjords and coastal areas would be severely overestimated using North Sea data. The similarity of $P/\overline{B}$ ratios between Sørfjord and the arctic Barents Sea (Denisenko 2001, Denisenko & Titov 2003)

Table 4. Average community productivity ($P/\bar{B}$) (yr^{-1}), biomass (B) (g m^{-2}) and production (P) (g m^{-2} yr^{-1}) from different areas/regions. Results from Sørfjord are given first, followed by a north to south gradient in latitude. B and P are given in wet weight. When originally given in other units, weight is converted from original data by factors from Brey et al. (1988), Christensen (1995) and Ricciardi & Bourget (1998) (see footnotes)

Area	$P/\bar{B}$	B	P	Source
Sørfjord, North Norway, 69° N	0.29	307	89	Present study
Barents Sea, 68–78° N	0.3	59.5		Denisenko & Titov (2003)
Southwestern Barents Sea, 69° N	0.25			Denisenko (2001)
Balsfjord, North Norway, 69° N		60[a]	17[b]	Bax & Eliassen (1990)
Disko Bay, Greenland, 69° N	0.1/1.9[c]		57 – 98[d,e]	Petersen & Curtis (1980)
Masfjord, West Norway, 60° N	2.6	58[e]	151[f]	Salvanes et al. (1992)
Baltic Sea, 55–60° N	0.32	53.8		Harvey et al. (2003)
North Sea, 52–62° N	5.0		70[d,e] + 28[d,e,g]	Steele (1974)
North Sea, 57° N	0.1–5.0	20 – 90[e]		McLusky & McIntyre (1988)
North Sea, 57° N	2.0–3.0		258[h]/160[i]	Christensen (1995)
North Sea, 51–57° N	1.9	76[f]	40[j]	Duineveld et al. (1991)
Northumberland, Great Britain, ca. 55° N	0.44		13.4[e]	Buchanan & Warwick (1974)
Grevelingen, Netherlands, ca. 52° N	2.6[f]	146[e]	354–404[e]	Wolff & de Wolf (1977)
Swansea Bay, Great Britain, ca. 51° N	1.28	55[e]	71[e]	Warwick & George (1980)
Cornwall, Great Britain, ca. 50° N	1.0[f]	93[e,k]	94[e,k]	Warwick & Price (1975)
Cornwall, Great Britain, ca. 50° N	1.0[f]	54.6[j,k]	54.3[j,k]	Warwick et al. (1979)
Bay of Somme, France, 50° N	0.5–2.8	7.8–128.3[j,l]	10.4–90.5[j,l]	Rybarczyk et al. (2003)
Bay of Fundy, Canada, 45° N			193	Wildish et al. (1986)
Browns Bank, Canada, 42° N			64	Wildish et al. (1989)
Cape Hatteras, USA, 35° N	1.3[f]	540[j,m]	400[j,m]	Aller et al. (2002)
Phangnga Bay, Thailand, 8° N			21[d,e]	Petersen & Curtis (1980)
Tasmania, ca. 41° S	1.5–11	5–133[e]	53–704[e]	Edgar & Barret (2002)
Southern plateau, New Zealand, 50° S	1.0	2.5[j]	2.5[g]	Bradford-Grieve et al. (2003)
Chile, 48–56° S	0.2	21–52[j]	3.9–11.1[j]	Thatje & Mutschke (1999)
Magellan, ca. 75° S	0.7	73[j]	51[j]	Brey & Gerdes (1999)
Weddell Sea, ca. 75° S	0.3	120[j]	36[j]	Brey & Gerdes (1999)

[a]Meio-, micro- and macrofauna
[b]$P/\bar{B}$ from Sørfjord, meio- and microfauna included in biomass and production, production estimated here
[c]Bivalvia and Polychaeta

[d]Converted from Brey et al. (l988)
[e]Converted from Christensen (l995)
[f]Estimated here
[g]Meiofauna
[h]Pelagic crustacea (except krill) included

[i]Crustacea excluded
[j]Converted from Ricciardi & Bourget (1998)
[k]Macrofauna defined as >0.5 mm
[l]Depending on feeding mode
[m]Macrofauna defined as >0.3 mm

supports the validity of the Sørfjord estimates. That the Sørfjord ratios appear to lie within a reasonable interval for a high latitude fjord make them valuable for other North Norwegian fjords and coastal areas with similar conditions when an approximate measure of production is required.

Biomass of benthic invertebrates varies greatly (Table 4), and depends on a number of factors related to food quality and quantity, substrate and top-down control from predators (Tumbiolo & Downing 1994). In their Balsfjord model, Bax & Eliassen (1990) used a benthic biomass of 60 g ww m^{-2}. This number was based on North Sea data and included micro- and meiofauna. Adopting the same biomass value, and considering also that micro- and meiofauna can contribute significantly to the total benthic biomass, would severely underestimate production in Sørfjord, where the biomass value (307 g ww m^{-2}) only includes macro-

fauna. Because of this high variability, biomass should always be measured for the area in question when $P/\bar{B}$ ratios are used to estimate production.

Species longevity and body size are often positively related to each other, while negatively related to $P/\bar{B}$ ratios (Zaika 1970, Banse & Mosher 1980). Not only do *Arctica islandica*, *Musculus niger* and *Ctenodiscus crispatus* attain high individual weights, but they also have a long life span compared to most other benthic animals. *A. islandica* can be over 200 yr old, while the other two reach about 20 yr. The potential of these species to attain high weight and/or high age is reflected in their low $P/\bar{B}$ ratios. All 3 species have $P/\bar{B}$ ratios not only lower than the community average, but also lower than the averages estimated for Mollusca and Echinodermata. With respect to *A. islandica* and *C. crispatus* the differences are high enough to severely overestimate production if separate species ratios (or ratios for

closer taxa) are not used. Such species/groups should therefore be treated with care when average $P/\overline{B}$ ratios are used to estimate production.

Most Polychaeta have low individual weights and short life cycles (Britaev et al. 2002). This combination of life strategies results in high $P/\overline{B}$ ratios (Zaika 1970, Banse & Mosher 1980), which is also shown in the present study where the Polychaeta $P/\overline{B}$ ratio was the highest of all statistical groups. The high biomass, mainly as a result of high abundance, combined with high $P/\overline{B}$ ratio made Polychaeta the most productive group. The high abundance observed in Sørfjord is comparable to other North Norwegian fjords (Oug 2000). High $P/\overline{B}$ ratios imply high renewal rates and the ability to replace biomass in a relatively short time (Tumbiolo & Downing 1994). Fjords dominated by small short-lived animals like Polychaeta can therefore be more easily affected by, and respond quickly to, short-term ecological changes. In Balsfjord the abundance of Polychaeta varied largely between years as a result of different nutrient regimes, with an increase from about 2000 to 4000 ind. m^{-2} from 1982 to 1985 (Oug 2000).

Relation between the benthic community and the environment

The well-mixed water column in Tarehola, combined with high abundance of diatoms (Heimdal 1974) and macroalgae, was expected to generate better feeding conditions for benthos compared to the other subareas where stratification occurs during summer. That no differences in total benthic biomass and production were observed could mean that there is a considerable lateral transport of organic matter inwards along the fjord, giving better feeding conditions than expected in the inner subareas. No organic measurements were made to support this. Polychaeta was responsible for the higher total abundance seen in Skognes compared with Tarehola; this is supported by the higher abundance in Tarehola when Polychaeta is disregarded. Polychaeta was present at all stations and the low correlation with the environmental variables was expected. However, most Polychaeta are known to prefer soft substrates, and the coarser sediments in Tarehola support a fauna with more typical epifaunal organisms as seen by the correspondence analyses. Data based on sampling gears that include more epifaunal organisms would possibly show more of the expected pattern.

An increase in depth is generally associated with a decrease in the quality and quantity of food reaching the bottom (McLusky & McIntyre 1988, Wassmann 1998), and this was believed to negatively affect biomass and production of the benthic community, partic-

ularly in Skognes, Njosken and Storura, which are stratified during summer. That no differences in biomass and production existed between the tested depth ranges could mean that: (1) stations were not deep or shallow enough to detect a trend, (2) the use of depth ranges was incorrect, or (3) food conditions were not as different as expected. Despite slow degradation of food at low temperatures (Tumbiolo & Downing 1994), differences are shown at similar depths in other subarctic areas (Curtis 1975). If food conditions were different, one would therefore expect biomass and production differences in the sampled depth range. In addition to the depth intervals 0 to 50 m and >50 m, depth was not significant for biomass and production when tested as a continuous co-variable in the ANCOVA. The results of the present study indicate that there is an increased deposition of organic matter below the more hydrodynamic zones and that the benthic feeding conditions in Sørfjord are relatively similar at all depths. Faecal pellets from krill and zooplankton are important food sources for benthos, and high sinking speed make them important in deep waters (Wassmann 1998). The high abundance of krill in the fjord (Zhou et al. 2005) and in stomachs of cod *Gadus morhua* (Kanapathippillai et al. 1994) and long rough dab *Hippoglossoides platessoides* (Mikkola 1996) caught in Njosken indicate that faecal pellets contribute significantly to benthos in the deep areas of the fjord when krill are present. Also, as this is an enclosed fjord system, the bottom area per depth stratum decreases rapidly with depth and could therefore counteract the decrease in sedimenting matter. That depth is significant for the biomass, production and abundance of Polychaeta, with the highest values at deep stations, was the opposite of what was expected from a nutritional point of view and is most likely a result of the finer sediments dominating at deep stations. The extreme dominance of Polychaeta in abundance also explains why total abundance is higher at deep stations.

Trophic role of benthos in Sørfjord

Benthic communities represent several trophic levels. In addition to herbivores and detrivores, predators and scavengers feeding on other benthic animals are included in the present study. Predatory Polychaeta constitute 10% of the Polychaeta abundance in Balsfjord (Oug 2000), and with their high abundance, biomass and production, predatory Polychaeta probably represent an important part of the benthic community of Sørfjord. Other typical predators and scavengers such as *Buccinum* sp., *Asterias* sp. and *Hyas* sp. are motile epifauna. These were insignificant in grab sam-

ples, but were caught in large quantities using other sampling equipment, e.g. bottom dredges and trawls (authors' pers. obs.).

Cod is the most abundant fish in Sørfjord. In 1990–1991, benthic organisms like large Polychaeta, *Hyas* sp., Anomura, Ophiuroidea, *Chlamys* sp. and *Buccinum* sp. constituted about 60% of the energy transferred to cod in Tarehola and Skognes (Kanapathippillai et al. 1994). This is in contrast to the situation reported by Hopkins et al. (1989), who suggested that benthos drives the microbial food web and does not support a commercially harvestable production in Balsfjord. *Arctica islandica*, *Ctenodiscus crispatus* and *Musculus niger* were not abundant in the diet of cod in Sørfjord (Kanapathippillai et al. 1994), suggesting that they constitute dead ends in the traditional food web and that a large amount of the biomass and production is limited to the microbial web and remineralisation. The overall yearly production of the benthic invertebrate community in Sørfjord of 4913 t is much higher than the average 200 t consumed by cod per year in the period 1990–1996 (Pedersen et al. 1997), leaving a great amount to other fish, benthic scavengers, benthic predators and microbes. In the Kattegat, benthic predators *Buccinum undatum* and *Asterias rubens* consumed more benthos than demersal fishes (Petersen & Jensen 1911), and consumption by other benthic invertebrates is probably more important than fish predation in Sørfjord as well.

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