Sources of variation in macrobenthic biodiversity and the implications for monitoring programmes in the Barents Sea

Nina Marie Bersås



Master thesis in Biology - Marine ecology
(60 credits)
Department of Aquatic BioSciences
Norwegian College of Fisheries Science
University of Tromsø

Spring 2009

## Contents

1 Introduction ..... 5
1.1 Marin biodiversity patterns over a range of scales ..... 5
1.2 The correlation between benthic variability and environmental variation ..... 6
1.3 Estimation of species richness and detectability ..... 7
2 Methods ..... 9
2.1 Site description and sampling ..... 9
2.2 Laboratory work and environmental variables ..... 10
2.3 Data analyses ..... 12
2.3.1 Marine biodiversity pattern over a range of scales ..... 12
2.3.2 The correlation between benthic variability and environmental variation ..... 13
2.3.3 Estimation of species richness and detectability ..... 17
3 Results ..... 20
3.1 Marine biodiversity patterns over a range of scales ..... 20
3.2 The correlation between benthic variability and environmental variation ..... 25
3.2.1 Beta diversity ..... 25
3.2.2 Multivariate analyses ..... 28
3.3 Detectability and estimation of total species richness ..... 35
3.3.1 Detectability ..... 35
3.3.2 Estimation of total species richness ..... - 37
4 Discussion ..... 41
5 References ..... 50
6 Appendix ..... 57


#### Abstract

In this thesis, several sources of variation which affect macrobenthic biodiversity was examined, in addition to addressing the resulting implications for monitoring programmes in the Barents Sea. Marine benthic biodiversity patterns at the time of sampling were examined across a range of scales, predefined by the study design. The benthic distribution was examined in relation to characteristics of organisms (e.g. functional groups) and environmental variation by multivariate analyses. Then the two main sources of error in monitoring programmes were addressed, spatial variation and detection error, e.g. the likely biodiversity in the Finnmark region IX at that time given that not all species and individuals present were sampled. Hence, probable species richness and detectability in addition to spatial variation was examined. Sources of bias and their importance for the statistical inference in the current monitoring programme were discussed. Suggestions based on the results are provided for how to develop a more robust monitoring programme, in order to separate the effects of confounded variables on soft-sediment benthic fauna.


## 1 Introduction

### 1.1 Marin biodiversity patterns over a range of scales

Marine biodiversity patterns are controlled by a complex of biological, environmental and anthropogenic factors operating at different temporal and spatial scales. It is difficult to explain the driving forces behind observed patterns in soft-sediment macrobenthic fauna in a dynamic biotope such as the Barents Sea. Usually, one is sampling remotely and blindly (Gray 2000). The high variability of marine ecosystems at most scales, means that it is difficult, but all the more important to tease apart the physical and biotic driving functions and to separate them from human impacts (Dayton et al. 2000). Faunal patterns and variability of soft-sediment macrobenthic faunas change with scales (Ellingsen 2001). Thus the observed benthic biodiversity patterns will differ according to scale, and under the influence of different sources of variation. In addition, the combined effects of several sources of variation may produce different benthic patterns at localities. Deducing the causal link of a mechanism in a marine system a posteriori would be impossible in most cases. Dayton et al. (2000) stressed the fact that environmental and human impacts often are synergistic, and a clear separation may not be possible, even when comparing disturbed to undisturbed reference sites. The term biological diversity is applied here according to the Convention on Biological Diversity (Article 2, CBD) "Biological diversity means the variability among living organisms from all sources including, inter alia terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (Magurran 2004).

The problem of scale, thus, also has fundamental applied importance. One principal question is how marine biodiversity should be measured in a given latitudinal area or within a monitored area. According to Levin (1992) there is no single natural scale at which ecological phenomena should be studied; systems generally show characteristic variability on a range of spatial, temporal and organizational scales. The concepts of scale and pattern are ineluctably intertwined. The description of pattern is the description of variation, and the quantification of variation requires the determination of scales (Hutchinson 1953; Denman \& Powell 1984 in Levin 1992). Hence the study scale should be specified when dealing with patterns of diversity (Gray 1997). This is why the chosen sampling design should correspond with the aim of biological monitoring programmes, i.e. on which scale does the patterns and processes we want to monitor occur? Monitoring is defined as the process of gathering information about some system state variables at different points in time, for the purpose of assessing system state and drawing inferences about changes in state over time. The systems of interest are typically ecosystems or components of such systems, e.g. communities and populations, and the state variables of interest include quantities such as species richness, species diversity, biomass and
population size (Yoccoz et al. 2001). Therefore the management decisions regarding chosen sampling effort, spatial scale and sample allocation will affect the likelihood of detecting species present at the time of sampling, in addition to affecting the likelihood of actually separating between effects from different sources of variation.

### 1.2 The correlation between benthic variability and environmental variation

Biodiversity patterns are correlated with environmental variables over a range of scales, from the immediate surroundings of benthic organisms to large scales including different habitats. Whittaker (1960 in Gray 1997) originally partitioned diversity into alpha, beta and gamma components. At small scales, where species are presumed to interact and compete for limiting resources, the diversity is called within-habitat or alpha diversity (Whittaker 1960, 1967 in Gray 1997). Beta diversity can be defined as the variability in species composition among sampling units for a given area, by measuring the average dissimilarity from individual observation units to their group centroid in multivariate space (Anderson et al. 2006). Thus, beta diversity is not a measurement of the number of species in different habitats in an area (Gray 2000), nor is it biodiversity measured on an intermediate scale. At large scales, i.e. regional scale, where evolutionary rather than ecological processes operate, the diversity is called gamma diversity ( $\gamma$ ) (Gray 1997).

Different environmental variables influence the distribution of taxonomical groups to a varying degree. Ellingsen (2001) found that polychaetes were the most common and widespread taxonomic group, whereas crustaceans and echinoderms were more restricted in their distribution. In a multivariate analysis based on Bray-Curtis similarities, Ellingsen \& Gray (2002) found that faunal patterns were more closely related to sorting and depth than latitude. Mollusks, followed by polychaetes, had the highest correlation to environmental variables. In another study, sediment and latitudinal gradients had a major effect on species composition and distribution of crustaceans, and sediment structure was found to be most important (Stransky 2007).

In several studies, characteristics of benthic taxa have been examined in order to gain knowledge of the ecological composition in the studied marine system (Brenke 2002; Buhl-Mortensen \& Mortensen 2004; Weslawski et al. 2003). The classification of benthic organisms into functional groups based on feeding modes, results in important ecological information regarding benthic distribution in relation to environmental variability. On local and regional scales, the composition and origin of the benthic fauna contains important information about the ecological processes in the monitored area (Brenke 2002). For this purpose, a database of functional groups was constructed with feeding modes and the mobility
of organisms classified according to their assumed ability to leave a disturbed and unfavorable habitat (see table A3.2).

### 1.3 Estimation of species richness and detectability

The likelihood of detecting a species in a given area is closely correlated with environmental heterogeneity, abundance and chosen sampling scale. Since both the distribution and abundance of species vary throughout the monitoring region, and the correct description of these patterns depends on the chosen study design, errors are quickly introduced when monitoring biological diversity. Therefore, the examination of total species richness and species detectability on differing scales in a given area is in fact complementary problems, all essential considerations when designing a monitoring programme. With respect to the question of how monitoring should be carried out, many existing programmes either ignore or deal ineffectively with the two primary sources of variation in monitoring data, spatial variation and detectability (Yoccoz et al. 2001). Detectability is defined as the probability that a member of a population of interest is detected during sampling. Detection error occurs because few survey methods permit the detection of all species in surveyed areas. The error of spatial variation in diversity estimation involves the inability to survey large areas entirely, resulting in a need to draw inferences about large areas based on samples of locations within those areas (Yoccoz et al. 2001).

It is usually impossible with sampling, regardless of effort, to obtain a complete list of species present in an area. Rare species have a low probability of being recorded, and thus their characterisation and observed distribution is directly linked to sampling intensity (Brown 1984; Gaston 1994 in Colwell \& Coddington 1994). Even after intensive sampling, some species are only represented by one or two individuals, commonly dubbed singletons or doubletons, or are detected in only one or two samples in a replicated sample set, commonly dubbed uniques or duplicates (Colwell \& Coddington 1994; Mao \& Colwell 2005). Enlarging the sample size yields additional individuals of these rare species and reveals additional new species that now represent new singletons and doubletons or uniques and duplicates. These are the workings of Preston's demon, the moving "veil line" between detected and undetected species as sample size increases (Preston 1948 in Mao \& Colwell 2005). For habitats such as marine sediments, one cannot expect to sample all the species. All that can be done is to estimate total species richness and the sampling effort needed to obtain reliable estimates of this richness (Ugland et al. 2003). Does the species richness and detectability vary among areas? Does varying detectability and spatial variation among areas affect the statistical inference?

So not only should biologists who design today's monitoring programs separate and quantify the effects on biodiversity patterns of the several confounding factors; spatial and temporal scales, varying detectability and environmental variation. They should also account for the fact that several
anthropogenic factors influence the biodiversity of benthic fauna. In the present study area, Finnmark region IX (Bakke et al. 1999; Bakke et al. 2001), the focus will be on three potential major sources of variation affecting the benthic fauna in the monitored region; oil excavation and gas industry, bottom trawling and predation by the red king crab (Paralithodes camtschaticus).

Olsgard and Gray (1995, in Gray et al. 1999) analyzed much of the data then available on the effects of oil and gas exploration on the Norwegian continental shelf, and found that the effects on benthic organisms to a radius of 3 km , i.e. ca. $30 \mathrm{~km}^{2}$, at a single field was a general pattern. Thus, the effects of excavation are found adjacent to installations. Regional monitoring was introduced in 1996, and makes it possible to examine the environmental effects of the offshore activities on a regional basis (Gray et al. 1999). The sampling sites cover all the oil fields and in addition a number of general reference sites are included. The purpose of these is to provide data for long-term changes such as those included by climate change (Gray et al. 1999). The new monitoring systems makes it far easier to examine trends in distribution patterns of fauna across the whole shelf and this provides knowledge of zoogeography and long-term changes which were not possible previously (Gray et al. 1999).

Dredging and bottom trawling are very destructive for the benthic fauna, but unfortunately few studies have documented marine habitats before they were trawled (Thrush et al. 1995, 1998, in Dayton et al. 2000). The Finnmark region IX has a substantial amount of fishery activities (von Quillfeldt \& Dommasnes 2005). In addition, there is a large standing-stock of the invasive king crab in the monitored region (Denisenko et al. 2008).

In every marine monitoring programme, one should consider effects from predation by an introduced key-stone predator on benthic fauna, not to mention the resulting dynamical population fluctuations between predator and prey. Introduced predators are assumed to have the largest effect on native communities (Elton 1958; Lodge 1993; Ross et al. in Lindal Jørgensen 2005), yet numerous top predators have been intentionally introduced for the purpose of fisheries establishment. Adult red king crabs are opportunistic omnivores (Cunningham 1969 in Lindal-Jørgensen 2005), feeding on the most abundant benthic organisms. King crabs have a seasonally variable consumption of prey such as bivalves and echinoderms (spring and summer in shallower waters $c .75-0 \mathrm{~m}$ ) and polychaetes (autumn and winter in deeper waters c. 200-300 m) (Lindal Jørgensen 2005). Hence, king crab predation is an unknown source of variation in the Finnmark region IX.

Since marine systems are complex and controlled by numerous factors, a full review of all potential sources of variation in benthic biodiversity patterns is beyond the scope of this thesis. The aim, therefore, is to address the chosen sources of variation which affect the statistical inference of the
monitoring programme, e.g. will it be possible to separate and quantify the effects from various sources of variation with the current study design?

First, it was examined if marine benthic biodiversity patterns at the time of sampling differed across the range of scales pre-defined by the study design. In the second part, the benthic distribution was examined in relation to characteristics of organisms (e.g. functional groups) and environmental variation by multivariate analyses. In the third part, the implication of varying species richness and detectability in addition to spatial variation was examined, e.g. the likely biodiversity at that time given that not all species and individuals present were detected and sampled.

Sources of error and their importance for the statistical inference in monitoring programmes were discussed. Suggestions based on the findings are provided for how to develop a more robust monitoring programme, in order to separate the effects of confounded variables on soft-sediment benthic fauna. The sampling design of the monitoring program will depend on the choice of error that should be considered when estimating biological diversity. Obviously, the extent and strength of the inferences drawn will vary depending on the design used (Yoccoz et al. 2001).

## 2 Methods

### 2.1 Site description and sampling

The quantitative monitoring survey Finnmark region IX was carried out over a spatial scale of c. 85000 $\mathrm{km}^{2}$ in the Barents Sea adjacent to the coast of Finnmark, and the three sampled regions covered roughly $11862 \mathrm{~km}^{2}$ (figure 1). The survey area is on the Northern part of the Norwegian continental shelf and the latitude range is approximately 170 km from North to South $\left(70^{\circ} 45^{\prime}\right.$ to $\left.72^{\circ} 15^{\prime} \mathrm{N}\right)$, whereas longitude spans approximately 500 km in a Eastern-western direction $\left(17^{\circ} 00^{\prime}\right.$ to $\left.32^{\circ} 10^{\prime}\right)$. The study area inhabits water masses with coastal and Atlantic water masses (Denisenko et al. 2008).

Benthic samples were collected from the Finnmark region IX on the Northern part of the continental shelf prior to oil and gas excavation in May 1998 and June 2000, as part of a monitoring project of the region that over time aims to discover potential negative effects due to oil and gas extraction. Thus, the analyzed data in this paper is from the existing quality-controlled OLF Database, owned by the Norwegian Oil Industry Association, on soft-sediment communities and sediment characteristics from the Norwegian continental shelf.


Figure 1
Map of sampled sites in 1998 and 2000 at the Finnmark region IX. The map was made in Telchart V version 1,47B (CMAP 5136), and thereafter edited in Paint. The South-western area: sample 1-32. The North-eastern area: sample 33-46. The North-western area: sample 47-55.

Biological, chemical and environmental samples were taken with a $0.1 \mathrm{~m}^{2}$ van Veen grab, 5 replicates were taken on each site for the analyses of benthic biodiversity. The data set consists of data from 55 sites in total, 30 sites sampled in 1998 and 25 in 2000 (figure 1). Only two sites were sampled both years, sample number 10 and 31, sample number 27 and 32 . Use of the differential global positioning system (GPS) in addition to the dynamical positional system onboard the research vessel, ensured that site placement was within $\pm 2 \mathrm{~m}$ accuracy from the planned position. Site water depth ranged from 154 to 371 m .

Biological samples were washed through a sieve with 1 mm mesh size, thus only macrobenthos (organisms $>1 \mathrm{~mm}$ ) were included in the survey. Then the organisms were fixed in formalin with added Bengal pink, for later identification to lowest possible taxonomical level. For chemical analyses, approximately 1 cm of the upper sediment layer was taken from three grabs on each site for analyses of metals and hydrocarbons. Sub-samples to determine sediment characteristics were taken from the upper 5 cm of 1 grab per site for analyses of sediment distribution (silt, clay, gravel and sand), kurtosis, sediment median grain-size, sorting, skewness and total organic matter (TOM). Samples for estimation of TOM were taken from three grabs per site.

### 2.2 Laboratory work and environmental variables

Later on in the laboratory, sediment characteristics were analyzed and determined. The gravel at size 2000-4000 $\mu \mathrm{m}$, was separated from the remainder sediment, and the cumulative percentage in weight
per site determined. Then the percent distribution of sand and silt-clay was determined by a mechanical separation of the sand fraction at size larger than $63 \mu \mathrm{~m}$, from the silt-clay fraction with size between 0 and $63 \mu \mathrm{~m}$. The remainder sand fractions were sieved on graded Wentworth sieves with different mesh sizes, at the range 63-2000 $\mu \mathrm{m}$ (Buchanan 1963). Afterwards the weights of all the fractions were determined, and cumulative weight distribution computed in percentage for each site. Then, calculations were done to determine values of kurtosis, skewness, sediment median grain-size and sorting (see tables A1 to A4). These must therefore be considered extrapolated environmental variables (Bakke et al. 2001). TOM was determined from sediment weigh loss after incineration (ignition loss) in an oven, where the sediment weight loss after incineration constitutes TOM (view Bakke et al. 1999; Bakke et al. 2001 for additional information on sampling and analyses). Sediment characteristics varied considerably throughout the survey area (silt-clay content 5.9-92.4 \%; TOM 2.1-11.3 \%; gravel 0-30.9 $\%$; for a full overview of environmental characteristics, see table A5). Sediments were more uniform in the Eastern part of the area, with substratum primarily consistent of coarse silt to medium-clay ( 3.81 to 5.81 , see table A1). The heterogeneous Western part had a patchy distribution with a mixture of sand, gravel and clay.

The applied methods were in concordance with the guidelines for biological monitoring of offshore installations set by the Norwegian Pollution Control Authority (NPCA, Norwegian abbreviation SFT, 1997) with the following exception of guideline 99:01: Placements of sites in an axe cross formation adjacent to an oil or gas installation is routinely imposed by SFT. However, the exact locations of the installations were not known at the time of the survey. Consequently a dispensation was given and the sites were placed in a grid formation along longitudes and latitudes (Bakke et al. 2000).

According to the SFT guidelines, taxa unsuitable for sampling by the applied methods were excluded from all data analyses (SFT, 1997). These taxa include (Nematoda, Foranminifera and Hydrozoa); colonial and primarily hard bottom organisms (Porifera, Bryozoa), pelagic crustaceans (Calanoida, Mysidacea, Hyperiidae, and Euphasiacea) and juvenile specimens. Some organisms were quantified, but not identified to species level (Platybelminthes, Nemertini, Tanaidacea and Tunicata). Taxa within the material listed as both one species (sp.) and many species (spp.) were pooled as spp. All taxa higher than species/genus level were excluded prior to data analysis; eventually there were 550 species left. Additional eight species which did not belong to the five main taxa examined were also removed (view appendix list A1) to ease comparison between various analyses. Species were pooled from the five replicated grabs taken at each site. In soft-sediment studies a single grab (sampling unit of $0.1 \mathrm{~m}^{2}$ ), samples only a small fraction of the species at a site because of small scale variation (Ugland et al. 2003). Pooling data across grabs evens out the high variability among them and gives a more representative picture of the community structure
at a site (Ellingsen 2002). The data analyses were primarily based on abundance or incidence. Hence there were 542 species left in the modified data file, ready for data analysis.

Profile, i.e. the angle of the sea floor, was assessed as a potential environmental variable. Sample placement were run in an Olex simulator (version 7.1) with a realistic 3D view of the seafloor topography, which showed that sample placement had only minor variance as they were placed either on flat substrate or on a gentle slope. Thus profile was excluded as a potential environmental variable.

Data on physical properties of the water masses (measurements of physical properties in water masses; Conductivity, Temperature and Depth; referred to as CTD) with information on salinity and temperature were not taken during the monitoring program. As a result, interpolated values were modelled based on CTD data found in databases from the area around the time of sampling. Since CTD's were not taken during the survey, environmental variables such as salinity and temperature were missing. To get an approximation of these two variables, they were modelled by linear interpolation in a linear regression model. The model was based on information found in oceanographic databases from the Finnmark region IX around the time of the surveys. Two databases were used; www.ices.dk and www.noaa.nodc, in addition to files from the Marine Research Institute in Bergen. The search for physical environmental data in the databases included data from May 15 to August 15 both years, thus oceanography data from a period around the time of biological sampling was downloaded. It was considered a trade-off between widening the search too much in time from biological sampling moment, and not having enough data points to model the oceanography of the region properly.

The data were then modeled in the linear model to give an approximate value of the oceanography for each site in the region. The final results were maps with approximate oceanographic properties by linear interpolation of data base information (see figure A1 and A2), in addition to approximate values for the environmental variables salinity and temperature (see table A5). In summary, environmental variables analysed were water depth, latitude, longitude, TOM, median grain-size, sorting (inclusive standard deviation), skewness, kurtosis, silt-clay, sand, gravel and approximate values of salinity and temperature. Average values of TOM were computed for each site based on three replicates.

### 2.3 Data analyses

### 2.3.1 Marine biodiversity pattern over a range of scales

Alpha diversity $(\alpha)$ is commonly measured as the number of species in a single sampling unit or at a site. Species diversity includes two aspects (Gray 2000); the total number of species in a given area (species richness) and the proportional abundances of the species (heterogeneity diversity). These univariate measures can be measured over different scales; a single point, samples, large scales,
biogeographical provinces and in assemblages and habitats. Based on the data from the Finnmark region IX, species richness and abundance were examined over a range of different scales: sample (which consists of 5 pooled replicates), within areas and between areas. The three examined areas were the South-western area, sample 1 to 32, North-eastern area, sample 33 to 46, and the North-western area, sample 47 to 55 (see figure 2). In order to avoid confounding between temporal and spatial variation, only spatial variation was examined. The chosen univariate methods of heterogeneity diversity were recommended in Gray (2000); Exp H', where H' is the Shannon-Wiener index, and $1 /$ Simpson's index. The two heterogeneity diversity indices were also computed for the five dominant taxonomical groups; polychaetes, mollusks, crustaceans, echinoderms and sipunculids.

### 2.3.2 The correlation between benthic variability and environmental variation

### 2.3.2.1 Beta diversity

Whittaker's original measure of beta diversity ( ${ }_{W}=\gamma / \bar{\alpha}$ or ${ }_{w}=(\gamma / \bar{\alpha})-1$ ) (Whittaker 1960; Whittaker 1972), the proportion by which a given area is richer than the average of samples within it, has been one of the most frequently used measures of beta diversity (Koleff et al. 2003). Beta diversity, $\beta$, can be measured in many different ways (Koleff et al. 2003; Magurran 2004) and at different scales. Beta diversity may also be based on differences in species composition between sites measured by dissimilarity (Legendre \& Legendre 1998; Magurran 2004).

Beta diversity can be defined as the variability in species composition among sampling units for a given area, and it can be measured as the average dissimilarity from individual observation units to their group centroid in multivariate space (Anderson et al. 2006). This method was used in this thesis, and has the added advantage over Whittaker's original measure that it can be used to test for differences in beta diversity among areas, through a multivariate test for homogeneity in dispersions. F-statistics was calculated to compare the average distance of observation units to their group centroid for the applied dissimilarity measure, and then p -values were obtained by permutation of least-squares residuals (Anderson 2006). Tw incidence-based dissimilarity indices were chosen; Bray-Curtis and Jaccard. For comparison, Chao's abundance-based Jaccard and Chao's bias-corrected dissimilarity was also examined. In addition, Euclidean distances based on normalized environmental variables were computed, in order to examine differences in species composition and environmental heterogeneity directly. Spatial coordinates were excluded as environmental variables in this analysis: "Note that what concerns us here is the structure within groups - the test says nothing about potential differences in location among groups in multivariate space" (Anderson et al. 2006).

### 2.3.2.2 Multivariate analysis

The same five dominant taxonomical groups were analyzed in the multivariate analyses as in the univariate analyses; polychaetes, mollusks, echinoderms, crustaceans and sipunculids. Explanatory analyses were done to examine the associate pattern and possible correlations between the response variables, which are the taxonomical groups. The scatter plot between the five groups showed nonuniform associate patterns between the response variables (see figure A3.1) and a canonical correspondence analysis was chosen. The scatter plot displayed a correlation for only two of the groups (see figure A3.1), mollusks and polychaetes are positively correlated with a pairwise Spearman rank value of 0.66 (see table A3.1).

In summary, environmental variables analysed were water depth, latitude, longitude, TOM, median grain-size, sorting (inclusive standard deviation), skewness, kurtosis, silt-clay, sand, gravel and approximate values of salinity and temperature (see table A5). However, some of the variables were confounded. Scatter plots of all pairwise combinations of the environmental variables showed that the associate pattern was correlated for some of these variables (see figure A3.2), and the Spearman rank correlation gave values of almost 1 for the variable silt-clay combined with grain-size and sand.

Hence, a stepwise model selection by Akaike's Information Criterion (AIC)(Ims \& Yoccoz 2006) was done in order to identify the best combination of parameters between response variables (all taxonomical groups) and environmental variables, explaining the most of the variance while reducing the numbers of confounded variables. The best fitted model included seven environmental variables; temperature, sorting, skewness, grainsize, latitude, longitude, and depth. In addition, stepwise model selection by AIC was also done for each taxonomical group. TOM was the most important environmental variable for the sipunculids. Therefore, TOM was also included after verifying that the variable was not confounded with any of the other chosen environmental variables. As a result, the final number of environmental variables was eight. The environmental variables were standardized to zero mean and unit variance in the CCA-analysis; this is done to obtain a common measurement scale for data analyses in the multivariate analyses. Finally, the five dominant taxa (response variables), the eight chosen environmental variables and spatial coordinates formed the basis of subsequent multivariate analyses. In addition, the categorical variables from the functional groups and the biogeographical classifications were included in the ordination. Spatial coordinates were not included in the dendrogram (see figure 9).

Much of the information was summed up in a multivariate analysis with direct ordination by Canonical Correlation Analysis (CCA), to explain the correlation between environmental variables and biodiversity patterns. CCA begins with two data matrices, species and environmental data, and seeks linear compounds which maximally reveal the joint or common structure of the two matrices (Austin

1976; Oksanen 2008). The purpose of ordination, beyond arrangements of ecological significance, is that of science: Understanding - in this case, understanding the complex patterns of natural communities in relation to environments that we see in the field (Austin 1976).

### 2.3.2.3 Functional groups

The classification of benthic organisms into functional groups was based on the work of Holte (1998) and Fauchald \& Jumars (1979). However, since the Finnmark region IX set consists of a wider range of phyla, categories were added and modified to fit the wide taxonomical range of organisms sampled. The different categories also had to be categorical variables, to accommodate the various data analyses. Feeding categories were (1) subsurface detrivor (all types of deposit feeding carried out in a buried state), (2) surface detrivor (all forms of deposit feeding on the seabed), (3) suspensivores (including both organisms which filters, such as sponges, and organisms which primarily collects food from the water masses with tentacles etc.), (4) carnivores (including scavengers, commensals, parasites and semiparasitic life forms) in addition to (5) omnivores. The omnivorous category consists of organisms with a mixed diet consisting of detritus in addition to scavenging and/or commensally and/or predacious feeding modes. See table A3.2 for the entire database with the functional groups.

Species which are both commensals and partially feed on the host were defined as omnivores if they eat detritus in addition. But species which only use sponges etc. as a vantage point for more favorable filtering were defined as suspensivores. Examples of this are the mollusk Heteronamia squamata and the amphipod Gitana abysscola (Buhl-Mortensen \& Mortensen 2005). These species are probably facultative commensals, but are considered suspensivores, since they are primarily filter feeders which do not depend upon a host for survival. The taxonomical groups also differ in terms of diversity in feeding mechanisms. Most families of marine gastropods are trophically homogeneous (Taylor \& Taylor 1977), so feeding mechanisms described on the family level may be generalized to all family members. On the other hand, amphipods are very diverse and feeding mechanism may differ within a family, therefore an affirmed feeding mechanism described on a genus level was preferred when ascribing taxa to a feeding category.

Amphipods in the family Cresseidae are very small and often overlooked in samples, therefore autecological literature is scarce. However, they share a strong resemblance in morphology with Stenothoidae; because they both have narrowed and lengthened mouthparts. Both cresseids and stenothoids are more chitinized than other amphipods and perfectly fused, adapted to strongly moved biotopes, such as among algae or on locations with many sessile epibenthic organisms (Krapp-Schickel 2005). There are discrepancies in regards to descriptions of feeding in Stenothoidae, with claims that for instance Stenothoe brevicornis is an obligate commensal of the cnidarian Actinostola callosa (Vader \& KrappSchickel 1996). The evolutionary development of obligate commensal crustaceans in a highly dynamic
biotope such as the Barents Sea is not likely. The Barents Sea is subject to not only high annual variability in terms of physical properties and environmental factors (Ingvaldsen et al. 2002), but also a variable biogeographical distribution of benthic organisms on a longer time scale in response to global weather patterns. Thus the evolution of obligate commensal crustaceans in the Barents Sea is not an evolutionary stable strategy, they would simply become extinct. These amphipods should be considered facultative commensal, in addition to other known feeding modes such as grazing and surface deposit feeding (Biernbaum 1979). Both Stenothoidae and Cresseidae are classified as omnivores in the database.

Amphipods in the family Lysianassidae can be either obligate scavengers or facultative scavengers, the latter also feeds on detritus (De Broyer et al. 2004; Klages et al. 2001). A transition to a detritus diet from a carrion diet seems likely in this family (Enequist 1949). Hence, all the sampled lysianassids were listed as omnivores due to their mixed diet consistent of both detritus and carrion. The only exception was Anonyx sp, which is considered to be primarily a scavenger and known to feed extensively on weakened animals as well (Klages et al. 2001; Steele \& Steele 1993).

The two most difficult species to assign to a feeding guild were the isopods Ischnomesus bispinosus and Dendrotion spinosum, since autecological information on deep-water fauna is scarce. When comparing the diets of pelagic and benthic isopods in the deep sea, Wolff (1962) found that most benthic asellotans have a mixed diet. They feed upon detritus, foranminiferans, phytoplankton, and scavenge and prey upon other crustaceans, polychaetes, sponges and hydroids. Both Dendrotionidae and Ischnomesidae are found primarily in the deep sea at depths greater than 200 m (Hessler \& Thistle 1975). Ischnomesidae is defined as an infaunal family, whereas Dendrotionidae is defined as an epibenthic family (Wilson \& Hessler 1987). Specimens of Ischnomesidae have shown some interest for carrion in captivity (Hessler \& Strömberg 1989), and have also been sampled with detritus in the intestines (Wolff 1962). Since Dendrotion spinosum have been sampled on location with enormous quantities of sponges, it has been theorized as to whether these isopods feed on sponges (Wolff 1962). As most benthic isopods are closely associated to the seabed with limited mobility, omnivore feeding mechanisms seems plausible in an oligotrophic environment such as the deep sea. Both species were assigned to the omnivorous feeding category.

The organisms were further classified into three different groups in terms of mobility, (i) non-mobile (sessile), (ii) discretely mobile (limited mobility) and (iii) mobile (capable of leaving an unfavorable location). Assigning organisms in diverse phyla to the same three mobility groups is not straightforward, due to substantial variation in size and mobility range. A crustacean may be very mobile compared to other small organisms, but when compared to considerably larger organisms such as brittle stars, have a short mobility range. The three before-mentioned mobility categories were considered the best solution in order to compare mobility over the diverse phyla.

When it comes to the applied definitions on the organism's movement, the term non-mobile includes only sessile organisms assumed to stay on one locality during the entire adult lifespan. These organisms will not be able to reposition themselves in response to disturbance. However, usage of the term is not as straightforward as one might expect. There is still some uncertainty as to whether for instance some polychaets, such as maldanids, have a limited form of mobility although they are considered sessile. The tubes of tubicolous polychaetes are often very long compared to the length of the animal which indicates that an apparently sessile, tubiculous polychaetes may in fact move slowly from one location to another (Fauchald \& Jumars 1979). Following the terminology in Fauchald \& Jumars (1979), these polychaetes were defined as non-mobile.

Discretely mobile organisms include those who burrows and move around in their immediate surroundings, and which may reposition within the same location in response to disturbance. The organism in the mobile category is considered capable of leaving an unfavorable location when needed. However, organisms with full mobility or swimming capability for only parts of their life cycle were classified as discretely mobile, since they are more dependent on the habitat and migration to a new locality is more difficult. For instance, the amphipods ampeliscids and phoxocephalids were defined as discretely mobile; they are more restricted to the sediment since only the adult males can swim (Enequist 1949 in Stransky 2007).

### 2.3.3 Estimation of species richness and detectability

### 2.3.3.1 Detectability

The software CARE-2 was used to implement a class of discrete-time closed capture-recapture models, developed by Chao (Chao \& Yang 2003) to estimate population size. However, in recent years scientists have used the CARE-2 to estimate species richness. In the context of estimating species richness, the detections of species encountered at different sample locations are analogs of the captures and recaptures of marked individuals at different sample times, hence names of a species served as an individual mark (Dorazio \& Jelks 2005). In this analysis, species is the equivalence of individual or animals. CARE-2 incorporates the use of covariates such as environmental variables or characteristics of a species.

In a closed capture-recapture model the underlying assumption is that there is no birth, death, or migration so that the population size is constant over trapping times (Chao \& Yang 2006). Obviously this is not the case in three examined areas of the Finnmark region IX, as these areas are part of an open marine system. Then again, since the sampling within each of the three areas was carried out over a short period of time, one can assume that during sampling the variance coming from birth, death or migration was negligible and therefore the capture-recapture models applicable. Dependence may be
caused by local dependence, the so called list dependence, within each animal (species) or by heterogeneity among animals (species). The capture intensity is allowed to vary with time, behavioral response and heterogeneity. The heterogeneity effect is modeled as a function of observable covariates but no assumptions regarding the time-varying function are made (Hwang \& Chao 2002).

Detectability analyses were performed separately for the three areas, to examine whether various characteristics (covariates) of organisms' affect their catchability and if this differs between the three monitored areas. The "individuals" (species) were heterogeneous in the sense that some were immobile organisms whereas others were mobile, a proportion living infaunal versus epibenthic. Is there a higher likelihood of sampling infaunal than epibenthic species? (Hypothesis H1). For the test of distribution in relation to sediment, the data entry was set as 1 for infaunal organisms and 0 for epibenthic organisms (beta1). Is there a higher likelihood of sampling immobile organisms than mobile ones? (H2). For the test of mobility, the data entry in CARE-2 was set as 1 for mobile organisms and 0 for non-mobile organisms (beta2). In addition, abundance was transformed $(\ln (x)+1)$ to fit the required input of the software CARE-2 and entered to examine whether abundance affected capture probabilities (beta3). Does the abundance of species in the three areas affect the catchability differently in the examined areas? It is assumed that the transformed abundance data functions as a continuous individual covariate, such as weight in mammals, so that the associated transformed abundance data of each species has an effect on the catchability.

### 2.3.3.2 Estimation of total species richness

Estimates of total species richness in the area was obtained by several methods; non-parametric estimators Chao2 and ICE (Colwell 2006), a traditional extrapolation of species accumulation curve (O'Dea et al. 2006) in addition to the T-S method developed by (Ugland et al. 2003). This method explicitly integrates the spatial heterogeneity of samples into the estimate of species richness for large areas by grouping areas into subsets based on shared environmental characteristics (O'Dea et al. 2006).

First, a traditional standard species accumulation curve was made by randomizing samples until the highest number of species was encountered, i.e. sampling with replacement. The curve was generated by the method described in (Ugland et al. 2003), this analytical expression is synonymous with Sobs in Colwell's Estimates, but with no variance, that is mean among runs. The species accumulation curve was extrapolated in order to estimate the species richness for a bigger area than sampled, by applying a semi-log estimate of the curve (O'Dea et al. 2006; Ugland et al. 2003). Thereafter the number of species was regressed against the logarithm of samples. Subsequently, the logarithm of the number of samples needed to cover three sampled areas was plotted into the regression equation to estimate true species richness.

In regards of the T-S projection, by applying the areal of the three different areas any patchiness in the distribution among the areas was examined (an underlying assumption of heterogeneity between the three regions, see figure 2). The species-area relationship and thus a new total-species curve (T-S curve) was extrapolated to estimate the likely true species richness in the three areas at the time of sampling (Ugland et al. 2003). The size of the areas ( $\mathrm{m}^{2}$ ) was obtained by using the Telchart mapping device to calculate distances in nautical miles (based on datum WGS 84), and then convert the resulting numbers to a metric scale.


Figure 2 Map of sampled sites in 1998 and 2000 at the Finnmark region IX. The map was made in Telchart V version 1,47B (CMAP 5136), and thereafter edited in Paint. The South-western area: sample 1-32. The North-eastern area: sample 33-46. The North-western area: sample 47-55. Green $=$ the South-western area, pink $=$ North-eastern and blue $=47$ to 55 .

Following the terminology in Ugland et al. (2003), two non-parametric estimators was applied to estimate true species richness and then compare with the T-S curve, by using the EstimateS free software with statistical estimation of species richness and shared species based on biotic sampling data (Colwell 2006). The applied estimators of species richness were Sobs $^{\text {(total number of all species }}$ recorded) and the non-parametric Chao2 estimator of true species richness (probable number of species present at the time of sampling).

The Chao2 estimator $={ }_{\text {Sobs }}+\left(\mathrm{Q}_{1}{ }^{2} / 2 \mathrm{Q}_{2}\right)$
(Equation 1)
$\mathrm{Q}_{1}$ and $\mathrm{Q}_{2}$ are the frequencies of uniques and duplicates. According to Colwell \& Coddington (1994), uniques are species found in one site, duplicates are species found in two sites, singletons are represented by a single individual whereas doubletons are represented by two individuals. The resulting species accumulation curves were based on means $\pm$ SD of 55 estimates based on 200 randomizations'
of sample accumulatio $n$ order (without replacement). The applied incidence-based coverage estimator, ICE, focuses on species found in $\leq 10$ sampling units (Colwell 2006).

All the data analyses were primarily done in Excel and the free-computing statistical software $\mathrm{R}(\mathrm{R}$ Development Team 2009). As previously mentioned, CARE-2 and EstimateS were used to compute detectability and estimate species richness, respectively.

## 3 Results

### 3.1 Marine biodiversity patterns over a range of scales

Local species richness or alpha diversity recorded in the Finnmark region IX varied noticeably (67 to 145 , see figure 3 below), and the abundance even more so ( 1 to 1537 , see figure 4 further down).

Sample 23, 33, 38 and 48 had a higher standard deviation than the remainder samples and displayed more variance between replicates for each sample.


Figure 3 Boxplot of species richness in each sample from a) SW area b) NW and NE areas (sample 33-46 and 4755 , respectively). Horizontal bars are median, both ends of the boxes mark the 25/75 percentiles, whiskers extend to 1.5 times box width (interquartile range), mild outliers (open circles) are between 1.5-3 times box width while extreme values (closed circles) are outside 3 times the box width.

The abundance varied considerably between samples. Numbers were particularly low for sample 28 and 29 in the South-western area, whereas the sample 39 and 43 had the highest abundance. The Southwestern area had the lowest abundance for pooled samples compared to the other areas, with 268 as the highest value in sample five. The highest abundance in a sample was recorded in sample 39 (pooled value of 308).


Figure 4 Boxplot of abundance in each sample from a) SW area b) NW and NE areas (sample 33-46 and 47-55, respectively). Horizontal bars are median, both ends of the boxes mark the $25 / 75$ percentiles, whiskers extend to 1.5 times box width (interquartile range), mild outliers (open circles) are between 1.5-3 times box width while extreme values (closed circles) are outside 3 times the box width.

Species richness and abundance showed different patterns in the Finnmark region IX. The species richness was markedly higher in the South-western and North-western areas than in the North-eastern area (see figure 5a) below). However, the abundance was highest in the North- eastern area and the North-western area, and lowest in the South-western area (see figure 5b) below). There was most variability within the South-western area.


Figure 5 Species richness a) and abundance b) as modelled interpolations between stations in the software R. Station placement is marked by black dots, and the three regions are encircled. This figure is based on an interpolation, and the data between the data points are generated. Abbrevations: NW $=$ North-western area, $\mathrm{SW}=$ South-western area and NE $=$ North-eastern area.

Species richness (S) and heterogeneity measures varied within and between areas. Values of heterogeneity measures were highest for sample 3,8 and 30 when computed with Shannon formula (see figure 6b) below), sample 8, 23 and 30 had highest values when applying the reciprocal of Simpson (see figure 6c) below). In general, values were higher when applying Simpson's measure of dominance in the South-western area and the North-western area, than in the North-eastern area, which in turn indicates the dominance of certain species in the North-eastern area when compared to the remainder areas, values were particularly low in sample 41 and 44.


Figure 6 Univariate measures of local community structure on all stations for the three examined regions; Southwestern (SW), North-eastern (NE) and North-western (NW). a) Species richness. b) The exponential of the Shannon formula (ExpH'). c) The reciprocal of Simpson's index ( $1 /$ Simpson).

Species richness and heterogeneity measures were examined for the five main benthic groups: polychaetes, crustaceans, mollusks, echinoderms and sipunculids (see figure 7 below). Heterogeneity diversity for the 5 dominant taxonomic groups varied more when computed with the reciprocal of Simpson, compared to the plot of Shannon formula (see figure 7 below). Of the 5 dominant taxonomic groups, polychaetes had the highest values of both species richness (see figure 7a below) and heterogeneity diversity when the exponential of Shannon formula was applied (see figure 7b) below). Interestingly, this was not the case in the heterogeneity diversity measure of dominance (see figure 7c
below). Crustaceans had the highest heterogeneity diversity values in the $1 /$ Simpson plot (sample 27 and 29). The latter is due to low crustacean abundance evenly distributed between several species.


Figure $7 \quad$ Univariate measures of local community structure divided in the 5 dominant taxonomical groups on all stations. a) Local species richness for the monitoring area. b) The exponential of the Shannon formula. c) The reciprocal of Simpson's index ( $1 /$ Simpson). Abbreviations; Pol = Polychaeta, Cru = Crustacea, Mol $=$ Mollusca, Ech $=$ Echinodermata and Sip $=$ Sipuncula.

On average, heterogeneity diversity in the $1 /$ Simpson plot was higher for polychaetes than crustaceans and the other groups. However, Polychaetes had very low values on sample 41 and 44 (see figure 7c), explained by the dominance of Maldane sarsi and Lumbrinereis spp. in these two samples (sample $41=$ $45 \%$, sample $44=40 \%$ ). A scatter plot with a pairwise comparison of the five groups in the Finnmark region IX showed that polychaetes and molluscs are positively correlated in the region (see figure A3.1),
which may indicate a similar distribution pattern in response to environmental characteristics. The two applied heterogeneity measures ( $1 / \mathrm{D}$ and $\mathrm{ExpH} H^{\prime}$ ) were strongly positively correlated with each other although these are different aspects of univariate biodiversity analyses.

Table 1: The percentage of species richness and abundance of the five dominant taxonomical groups.

|  | South-western area <br> Species <br> richness |  | Abundance | North-eastern area <br> Species <br> richness |  | North-western area <br> Species |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | :---: |
| Abundance | richness | Abundance |  |  |  |  |  |
| Polychaeta | 55.2 | 66.4 | 53.1 | 66.7 | 58.0 | 59.4 |  |
| Mollusca | 21.8 | 10.8 | 18.5 | 21.1 | 14.0 | 19.9 |  |
| Crustacea | 19.3 | 12.4 | 21.3 | 6.4 | 21.2 | 10.2 |  |
| Sipuncula | 2.0 | 7.8 | 4.4 | 5.4 | 3.8 | 7.5 |  |
| Echinodermata | 1.7 | 2.6 | 2.7 | 0.5 | 3.0 | 3.1 |  |

The North-eastern area had the highest abundance of both polychaetes and mollusks when compared to the other two areas, but the abundance of crustaceans, sipunculids and echinoderms were markedly lower (see table 1). The lowest species richness of polychaetes was found in the North-eastern area, but species richness of mollusks was higher than in the North-western area. In the North-western area, echinoderms were most abundant and had highest species richness here when compared to the remainder areas. Species richness of polychaetes was highest here. The South-western region had markedly lower abundance of mollusks compared to the other groups. However, species richness was highest for mollusks in this area.

### 3.2 The correlation between benthic variability and environmental variation

### 3.2.1 Beta diversity

In concordance with the analyses in Anderson et al. (2006) ; the null hypothesis of homogeneity in the multivariate dispersions among areas were tested both for compositional and environmental data. For the species composition, differences between areas were tested on the basis of the Sørensen dissimilarity measure. Subsequently, the null hypothesis of environmental homogeneity was tested by computing Euclidean distances to group centroid on the basis of normalized environmental data.

The null hypothesis of homogeneity in compositional data among areas was rejected, since there were significant differences among regions in biotic variability (see table 2 below). There was highest variability in the South-western area, followed by the North-eastern area and then the North-western area. The results from the test of environmental homogeneity mirrored the analysis of compositional data, as there were statistically significant differences between all the three areas in concordance with that found in the benthic fauna (see table 3 further down). In addition, the multivariate dispersion
patterns of environmental variation among areas were similar, as the biggest area (South-western) had the highest degree of variability, followed by the intermediate area (North-eastern), and then the Northwestern area (see figure A3.1). But the results for the test of environmental homogeneity differed from the test of homogeneity in biotic variability when it came to pairwise comparison between the Northeastern and North-western areas. There was no statistically significant difference in environmental heterogeneity between the North-western and North-eastern area (pairwise comparisons, $\mathrm{P}<0.16$, table 2).

Table 2: The results of tests for homogeneity of multivariate dispersions based on several dissimilarity measures. Where there was a statistically significant overall F-ratio comparing group ( $\mathrm{P}<0.05$, Permutation test for homogeneity of multivariate dispersions with permutations: 9999). Numbers 1-3 corresponds to the three areas; 1) South-western, 2) Northeastern and 3) North-western. Underlining bars indicate groups that were not statistically significantly different.

| Distance measure | F |  |  |
| :--- | :--- | :--- | :--- |
| Sørensen | 123 | 17.651 | P-value |
| Jaccard | 123 | 40.624 | $0.0001^{* * *}$ |
| Chao's bias-corrected | $1 \underline{23}$ | 19.911 | $0.0001^{* * *}$ |
| Chao's abundance-based Jaccard | $1 \underline{23}$ | 18.896 | $0.0001^{* * *}$ |
| Euclidean - normalized | $1 \underline{23}$ | 12.606 | $0.0001^{* * *}$ |

Thus three of the applied dissimilarity measures showed the same pattern among areas, namely Sørensen, Jaccard and Euclidean distances (see table A3.1). The biggest area sampled (SW) showed the highest degree of variation, followed by the intermediate area (NE) and then the smallest area sampled (NW). This pattern was also depicted when applying Whittaker's beta diversity ( $\mathrm{B}_{\mathrm{w}}$ ) measure (see table 3); the South-western area had the most variability. In concordance with the results in Anderson et al (2006), there was a general agreement in the rank order of measures of beta diversity, using Sørensen, Jaccard and $\mathrm{B}_{\mathrm{w}}$.

Table 3: Average species richness $(\bar{\alpha})$, gamma diversity $(\gamma)$ and beta diversity $\left(\beta_{\mathrm{w}}=(\gamma / \bar{\alpha})-1\right)$.

| Area | $\bar{\alpha}$ | $\gamma$ | $\beta_{\mathrm{W}}$ |
| :--- | ---: | ---: | ---: |
| South West (1-32) | 100 | 455 | 3.5 |
| North West (33-46) | 84 | 226 | 1.7 |
| North East (47-55) | 111 | 237 | 1.1 |

However, although the patterns of multivariate dispersions in biotic data were similar, the results were somewhat different when applying the bias-corrected version of Chao and the abundance-based Jaccard. When applying the abundance-based Jaccard dissimilarity measure, the pattern was inverse compared to those previously displayed. Whereas the incidence-based Jaccard measure showed the greatest variability in the biggest area and then receded (see figure 8a below), the abundance-based Jaccard showed the opposite (see figure 8 b below).


Figure 8 Boxplots of the multivariate dispersion to group centroid for the three areas. a) Jaccard; b) Chao's abundance-based Jaccard and c) the bias-corrected Chao.

The values were lowest for the South-western area, followed by the intermediate area North-eastern area and with the highest degree of variability in the North-western area. This could be due to higher and more variable abundance of the benthic fauna in the North-eastern and North-western area. The bias-corrected version of Chao which accounts for unseen species in the samples showed the most
variability in the South-western area, than followed by the North-western area and then the Northeastern area (see figure 8c), a different pattern than previously shown for the other dissimilarity indices. The lowest values computed for the North-eastern area was possibly due to more homogenous environmental conditions there.

The unbalanced study design could have affected the observed dissimilarity patterns between areas. Number of samples in the biggest area, the South-western one, amounted to a total of 32 samples, whereas there were 14 samples in the North-eastern area and only nine in the North-western area. In concordance with the data analysis in Anderson et al. (2006), the results from the Sørensen dissimilarity measure was regressed against the normalized environmental variables based on Euclidean distances.

The regression of biotic variables against the environmental data resulted in a high value of 0.98 for the coefficient of determination $\left(R^{2}\right)$. In order to examine the importance of the unbalanced study design on the observed pattern of multivariate dispersions in biotic data, the bias-corrected Chao dissimilarity measure was regressed against the abundance-based Jaccard (this measure reduces the sample-size bias, view Anderson et al 2006 for further details). When the results from the three areas were regressed against each other with a simple bivariate regression, the $\mathrm{R}^{2}$ coefficient of determination was 0.92 . However, since there were only three data points in the regression, whether or not the unbalanced study design was the driving force behind the observed patterns could not be resolved.

### 3.2.2 Multivariate analyses

In the cluster analysis based on chi-square distances for the dominant taxonomical groups, there were several easily identified outliers markedly dissimilar from the rest of the samples (see figure 9a) below). Sample 2, 18, and 55 are outliers markedly different from the remainder samples. Overall, the samples from the North-eastern area is clustered together on the right side of the figure (sample 35 to 43 ), whereas the samples from the two Western area are more scattered, although samples 50, 51 and 52 from the North-western area are clustered together.


Figure 9 Cluster analyses. a) Chi-square distances for the five dominant taxonomical groups in all samples; polychaetes, mollusks, crustaceans, echinoderms and sipunculids. b) Euclidean distances for normalized environmental variables in samples. The best subset of environmental variables excluding spatial coordinates was chosen (view methods for details).

Regarding the cluster analysis of the environmental characteristics based on Euclidean distances, sample 2 was an outlier in conformity with the chi-square distances on taxa (see figure 9b). Sample 2, 7 and 9 were outliers markedly dissimilar from the other samples. There was a considerable dissimilarity among samples; samples were clustered together in three groups according to similarity. In concordance with the dissimilarity of taxa, the samples from the North-eastern area were grouped together on the right (sample 38 to 43). In addition, samples from the North-western area were grouped together on the left (sample 52 to 51).
a)

b)


Figure 10 Non-metric multidimensional scaling figures (NMDS) in two dimensions (function isoNMDS in R), which show the multidimensional distance between sampling samples according to group abundance. a) All samples included. b) The outliers; sample 2, 11, 47 and 55 have been removed and the spread of the samples are improved.

The non-metric multidimensional scaling (NMDS; figure 10) shows the distance between samples according to species abundance and retained the total distance in the multidimensional sampling space in the reduced dimension with a substantial amount of stress. The NMDS stress was relatively high, with a value of 18.07. Hence, even though the NMDS retained the multidimensional relationship between samples in a multidimensional space based on the five 5 pooled taxonomic groups, the high stress value indicated a poor two-dimensional display of the high multidimensional variation in the data set.

Polychaets ends up being localized centrally in figure 11 below, which is expected as this is the dominant group in most of the samples. Thus the samples in the middle of the figure are mostly dominated by polychaets, since they are placed adjacent to this group. However, a sample with all groups present and with the same abundance would also be in the middle (Nigel Yoccoz, pers. comm.)The size of the triangles indicates the weight of the groups when it comes to abundance, and the big triangle of the polychaets shows the dominance of this group compared to the other groups. In comparison, the echinoderms are the least abundant organisms in the samples and therefore placed in the outskirts of the figure. Mollusks are the second dominating groups in terms of abundance, as shown by the second largest triangle. The samples placed in between polychaets and mollusks are the ones which are influenced by both groups. Interestingly, these samples are mostly found in the Northeastern area, with the exception of sample 41 and 44 which are placed between polychaetes and sipunculids. So the samples from the North-eastern region are clustered together, which indicates a more homogenous distribution, whereas the samples from the Western regions are scattered which in turn points to higher heterogeneity.


Figure 11 Correspondence analyses (CA) plot of the 5 taxonomical dominant groups in all samples; polychaets, crustaceans, mollusks, echinoderms and sipunculids. Northeast samples are circled.

The outliers are placed in the outskirts of the CA plot (figure 11), and these are sample 11, 18 and 55. Two more outliers were identified in the NMDS plot (sample 2 and 47, figure 10). The outlier seen in the upper left corner of figure 11 (sample 55) is dominated by mollusks, sipunculids and polychaetes. The outliers 2 and 11 appear to be primarily dominated by crustaceans rather than by echinoderms. But a closer look in the RGL device (3D) actually shows that sample 2 also have a high proportion of echinoderms, as it is positioned closely to the group in a multidimensional space. Sample 47 is equally influenced by crustaceans, mollusks and echinoderms since it is placed in the center of these three groups. The outlier 18 is dominated by sipunculids.


Figure 12 Triplot from a canonical correspondence analysis (CCA) showing samples (sample 1 to 55, black), taxonomical groups as response variables (red), environmental and categorical variables (blue). Total variation explained is $38.69 \%$. CCA-1-axis explains $24.48 \%$ and the CCA2-axis $7.23 \%$.

The total amount of variation by direct ordination was 38.69 percent. There were 4 CCA-axes on constrained (shared) environmental axes presented in triplots with an ecological gradient along each CCA axis. Only the triplot of the main ordination axes CCA1 and CCA2 are included here (see figure 12), since they explained most of the variation ( 42.48 and $7.23 \%$ respectively, view appendix for the triplot with CCA2-axis and CCA3-axis; see figure A3.3). The gradient associated with the main ordination axis (CCA1) separates environmental variables skewness, latitude and longitude from the remainder variables (figure 12). The length of the arrow shows the strength of the correlation between the variable and the ordination; hence sorting, longitude and TOM are important constraints. CCA1 axis (the environmental gradient) decreases when latitude, skewness, sorting and temperature increase. The CCA1 axis increases with longitude, grainsize and TOM. Depth is placed in the middle of the figure and connects the vectors.

Sorting was almost parallel to CCA1-axis, sorting and temperature decreased with increasing longitude in the Finnmark region IX. Echinoderms were predominately affected by temperature and sorting, as seen by the placement. TOM ran almost parallel with the CCA2-axis and increased when longitude decreased, e.g. the organic content increased from the East towards the West along an ecological gradient. The abundance of sipunculids was strongly positively correlated with TOM. The distribution of crustaceans was probably determined by several environmental variables, since this group was placed further from the vectors. Skewness was positively correlated with the latitude and these vectors influential on mollusks, as previously mentioned the samples clustered together were primarily from the

North-eastern area. Polychaetes were the dominant group given the groups placement in the middle of the CCA plot, the abundance was positively correlated to grainsize.


Figure 13 A Canonical Correspondence analysis (CCA) plot (sample 1 to 55, black), taxonomical groups as response variables (red), environmental and categorical variables (blue). The percentage of variation explained in figure 12 is $48.87 \%$. CCA-1-axis explained $25.27 \%$ and the CCA2-axis $13.04 \%$. Abbreviations'; TOM: (total organic matter), Grain: grainsize, Long: longitude, Ssdet: sub-surface detrivores, Lat: latitude, Skew: skewness, Sort: sorting, Carn: carnivores, Temp: temperature, Susp: suspensivores, Omn: omnivores, Sdet: surface detrivores. Temp and Susp are placed on top of each other.

The total amount of variation by direct ordination was $48.87 \%$ (figure 13). In concordance with the first ordination plot, CCA1-axis and CCA2-axis had the highest percentage of variation explained (25.27 and 13.04 \% respectively, see appendix for the triplot with CCA2-axis and CCA3-axis; figure A3.4). As seen in the CCA plot of the feeding guild (figure 13), subsurface detrivores dominated in the samples from the North -eastern area, this feeding mode was positively correlated with longitude, e.g. numbers increase from the West to the East in the Finnmark region IX. Interestingly, subsurface omnivores shared an almost inverse relationship with the surface omnivores and latitude. Thus numbers of surface detrivores increased with decreasing latitude, e.g. an overweight in the Southwestern area. However, samples from the two Western areas were more scattered than the samples from the North-eastern area.

Surface omnivores, suspensivores, carnivores and surface detrivores were positively correlated towards the West in the Finnmark region IX, as the samples adjacent to vectors are from the Western areas. Temperature and suspensivores are strongly correlated. Not surprisingly, crustaceans were predominated by suspensivores, but also by omnivores and carnivores. Echinoderms had a
predominance of omnivores, but also had organisms with a carnivorous feeding mode. Polychaetes were localized in the middle and had diverse feeding modes. Sipunculids are surface detrivores, but since TOM is a very influential variable on the distribution of primarily this group alone, sipunculids were localized closer to the vector of TOM in multivariate space.

The importance of three different mobility modes for the benthic response variables was examined, in addition to the eight predictor variables previously examined (see figure 14 below). Total amount of explained variation by the predictor variables were $43.25 \%$, CCA- 1 -axis explained $25.13 \%$ and the CCA2-axis $9.83 \%$ (see appendix for CCA-triplot of CCA-axis 2 and 3; figure A3.5). The gradient associated with the main ordination axis (CCA1) separates environmental variables skewness, latitude and longitude from the remainder variables (figure 14). The same trend was shown in the previous plot, where the gradient associated with the main ordination axis CCA1, separated these variables in addition to sub-surface detrivores from the remainder predictor variables.

The vector of non-mobility ran almost parallel to the CCA2-axis, in concordance with surface detrivores in the previous plot. Non-mobility and depth were positively correlated, but less important in explaining total variation compared to sorting and longitude (short arrows). Temperature, mobility and discretely mobile were strongly positively correlated. Sorting was also positively correlated with these three variables. Both crustaceans and echinoderms had mostly mobile and discretely mobile organisms, as seen by the group's placement and direction of the vectors. Sipunculids are the only completely non-mobile group, thus they are placed at the end of non-mobility vector. Polychaetes are placed in the middle of the plot where the vectors are connected. This group had a higher number of non-mobile organisms than mobile and discretely mobile. Mollusks were dominated by the environmental variables skewness, latitude and longitude to an extent where these constraints dominated in the ordination for this group, since the CCA ordination presents the best possible combination of the three-dimensional space in a reduced two-dimensional plot.


Figure 14 A Canonical Correspondence analysis (CCA) plot (sample 1 to 55, black), taxonomical groups as response variables (red), environmental and categorical variables (blue). The percentage of variation explained in figure 11 is $43.25 \%$. CCA-1-axis explained $25.13 \%$ and the CCA2-axis $9.83 \%$. Abbreviations'; TOM: (total organic matter), Grain: grainsize, Long: longitude, Lat: latitude, Skew: skewness, Sort: sorting, Temp: temperature, Dmob = discretely mobile, Mob $=$ Mobile, Nmob $=$ Non-mobile.

As previously shown in the pairwise scatter plot of benthic groups (see figure A3.1), polychaetes and molluscs were positively correlated in the region with a rank value of 0.66 . The distribution of echinoderms was correlated with longitude ( -0.66 ), their abundance decreases from west to east (see table 1). Temperature was strongly correlated with longitude ( -0.87 ) (see figure A3.1), the approximate values of temperature decreases towards the east in the Finnmark region IX both years (see figure A1). Echinoderms were also correlated with longitude.

### 3.3 Detectability and estimation of total species richness

### 3.3.1 Detectability

In the North-western area, there is no difference in catchability between epibenthic and infaunal organisms and the regression coefficient beta 2 was very small, so the effect of mobility is almost negligible (see table 4 below). When the coefficient of $\beta>0$, the larger the covariate is, the larger the capture probability is (Chao \& Yang 2006). However, the North-western area had the highest proportion of mobile and epibenthic organisms when compared to the other areas, whereas the beta 2 coefficient (H2) was not significant in the North-eastern area, the likelihood was equal both for mobile and immobile organisms (see table 4). This area had the highest catchability of infaunal organisms when compared to the other areas. When $\beta<0$ then the larger the covariate is, the smaller the capture probability is (Chao \& Yang 2003). High abundance had highest effect on the catchability of organisms
in the North-western area; a beta3 value of 1.46 is the effect for a unit change in abundance. In the North-western area, the beta3 value was 1.17 whereas it was lowest in the South-western area with 0.82 (table 4). Higher abundance increased catchability of organisms in all the regions, but the effect was most pronounced in the North-eastern and North-western areas.

Table 4: Maximum likelihood estimates (with SE) of model parameter regression coefficients with and without time effects from each of the three areas (South-western, North-eastern, North-western). Model parameters: $a=$ intercept, $v=$ behavioral response, $\beta_{1}=$ infaunal/epibenthic, $\beta_{2}=$ mobility, and $\beta_{3}=$ abundance. $\mathrm{h}=$ heterogeneity, $\mathrm{b}=$ behaviour and t $=$ time.

| Area | Model | $a$ | $v$ | $\beta_{1}$ | $\beta_{2}$ | $\beta_{3}$ |
| :--- | :--- | :---: | :---: | :---: | :---: | :---: |
| SW | $\mathrm{M}^{*}$ bh | $2.66(0.17)$ | $2.60(0.17)$ | $-0.51(0.08)$ | $-0.80(0.06)$ | $0.82(0.03)$ |
| SW (time) | $\mathrm{M}^{*}$ th | $-1.07(0.07)$ |  | $-0.58(0.06)$ | $-0.79(0.06)$ | $0.91(0.03)$ |
| NE | $\mathrm{M}^{*} \mathrm{~h}$ | $4.35(0.17)$ |  | $-0.23(0.13)$ | $-0.03(0.00)$ | $1.14(0.06)$ |
| NE (time) | $\mathrm{M}^{*}$ tbh | $5.38(0.44)$ | $0.45(0.28)$ | $-0.24(0.12)$ | $-0.02(0.09)$ | $1.17(0.05)$ |
| NW | $\mathrm{M}^{*} \mathrm{~h}$ | $4.38(0.22)$ |  | $0.01(0.04)$ | $0.06(0.30)$ | $1.39(0.07)$ |
| NW (time) | $\mathrm{M}^{*}$ tbh | $5.92(0.32)$ | $0.20(0.28)$ | $0.00(0.08)$ | $0.06(0.21)$ | $1.46(0.07)$ |

In the North-eastern and North-western area, the most complex models converged ( $M^{*}$ tbh; table 4). The parameter $v$ represents the effect of a recapture, e.g. the behavioral response effect. Thus $v>0$ (table 4) is an estimate of the recapture-likelihood. The higher the value of $v$ is, the higher the likelihood is of a recapture. Since the input in the analysis was not individuals, but species, the output can be interpreted as the likelihood of re-sampling a species in an area given the values of the covariates. In the South-western area the most complex model including time effect did not converge, but the $\mathrm{M}^{*}$ bh model gave a $v$-value of 2.60 (table 4). Possibly, the amount of spread in the data material was too high for the software to converge the most advanced model in the biggest area. However, the parameter $v$ was 0.45 in the North-eastern and 0.20 in the North-western area. These results are not indicative of a behavioral component in the organisms, but are estimates of an organism's recapture-likelihood. The likelihood of an organism to be captured and recaptured was highest in the South-western area with the most samples, followed by the intermediate area (NE) and finally by the North-western area with the lowest number of samples. In summary, both the number of samples in an area and the abundance of an organism affect the cathability and thus the likelihood of being captured and recaptured in an area.

The estimates were linked to sampling effort and are also a measure of the species richness in the areas. Then from the summary of model fitting the estimated population size under the selected model $\mathrm{M}^{*} \mathrm{bh}$ in the South-western area is 792.97 (s.e. 96.78 ) with a $95 \%$ confidence interval $649.78-1040.77$ (see table A2.1). In the North-eastern area the estimated population size under the selected model was 388.28 (s.e. 60.48 ) with a $95 \%$ confidence interval $305.86-554.72$ (see table A2.4). In the Northwestern area the estimated population size under the selected model was 368.87 (s.e. 49.37) with a $95 \%$ confidence interval 301.48 - 501.18 (see table A2.6). Consequently, the estimated species richness was 792 species, 337 estimated additional species in the South-western area ( $M^{*} 0$ model 455 , see table

A2.1). The estimated number of additional species were 163 in the North-eastern area ( $\mathrm{M} * 0$ model 225, see table A2.4) and 131 additional species in the North-western area ( $\mathrm{M}^{*} 0$ model 237 , see table A2.6).

### 3.3.2 Estimation of total species richness

The non-parametric species estimators gave results in the same order of magnitude; Chao2 estimates gave a probable total species richness of 734 species and ICE 683. The curve of Chao2 does not level off, whereas the ICE estimator appears to approach an asymptote (see figure 15a below). The graph of singletons level out and show a slight increase towards the tail whereas the graph of doubletons declines towards the tail (see figure 15b below). The curve shapes of uniques and duplicates are almost identical to those of the singletons and doubletons, the graph of uniques levels out with a slight increase towards the tail and the graph of duplicates levels out and declines toward the tail of the graph (see figure 15c).

Conversely, the two non-parametric estimators Chao2 and ICE resulted in estimates of total species richness in the same order of magnitude, compared with results from the extrapolated species accumulation curve and T-S curves method.


Figure 15
Species accumulation curves. The estimators of total species richness were Chao2 (lower bound estimator with standard deviations) and ICE (estimates based on species found in ten or fewer sampling units with standard deviations). Plotted values are means of 55 estimates based on 200 randomizations of sample accumulation order (without replacement). Sobs(Mau tau: analytical expression without variance) b) Singletons ( $21.4 \%$ ) are found in only one location, doubletons ( $9.8 \%$ ) are found in two locations c) Uniques ( $25.6 \%$ ) are species sampled only once, duplicates ( $9.97 \%$ ) are sampled twice. The Chao2 estimator is based one the ratio between uniques and duplicates, respectively.


Figure 16
a) The species accumulation curves for all combinations of the three areas sampled in the Finnmark region IX (North-western, South-western and North-eastern areas); the number of species are plotted against the number of samples. b) A semi-log approximation of the species accumulation curves combining all areas, the number of species were regressed against the logarithmic number of samples.

On figure 16a), the $S / \ln (x)$ ratio of the standard species accumulation curve abates towards the tail of the graph, but the graph does not reach an asymptote. The traditional extrapolation of the standard species accumulation curve when the number of species were regressed against the log number of samples, gave an estimate of 2164 species for the area covered by the three regions, had the entire area been sampled. Since all the pooled samples consisted of five replicates of $0.1 \mathrm{~m}^{2}$ each, it would take two pooled samples to cover $1 \mathrm{~m}^{2}$. The three examined areas covered roughly $11862 \mathrm{~km}^{2}$ when added together, which in turn equals $118620000 \mathrm{~m}^{2}$. Since all the pooled samples consisted of five replicates of $0.1 \mathrm{~m}^{2}$ each, totally $0.5 \mathrm{~m}^{2}$, it would take two pooled samples to cover $1 \mathrm{~m}^{2}$.
$11863 \mathrm{~km}^{2}=118620000 \mathrm{~m}^{2}$
5 replicates $* 0.1 \mathrm{~m}^{2}=0.5 \mathrm{~m}^{2}$ pooled sample
$0.5 \mathrm{~m}^{2 *} 2=1 \mathrm{~m}^{2}$ sample coverage
$118620000 \mathrm{~m}^{2 *} 0.5 \mathrm{~m}^{2}=59310000$ number of samples needed to cover $118620000 \mathrm{~m}^{2}$
$117.39 * \ln (\mathrm{x})+63.304=\mathrm{y}$
(Equation 2; see figure 16b))
$117.39 * \ln (59310000)+63.304=2164$ estimated number of species.

Consequently, the number of samples needed to cover all the three areas was $59310000(118620000$ $\mathrm{m}^{2} * 0.5 \mathrm{~m}^{2}$ pooled sample) and the estimate of total species richness were calculated as follows: $117.39 * \ln (59310000)+63.304=2164$.

However, this traditional approach does not account for the spatial heterogeneity among the different areas sampled. Hence, the species richness of all the three areas in the Finnmark region IX was examined with an emphasis on the spatial and environmental heterogeneity observed between areas (see table A5).


Figure 17 a) Species-accumulation curves for all combinations of the three examined areas in the Snow white monitoring area. The new total species projection curve (T-S curve) is the weighted line drawn through the average total number of species in all three combinations of three areas. b) Regression of the average number of species in all combinations of the three examined areas, against the logarithm of the number of samples in each of the areas.

As seen in figure 17a, the species-accumulation curve becomes steeper every time a new combination of sub-regions is added. Following the terminology in (Ugland et al. 2003), the new total species projection curve (T-S) is a smooth curve drawn through the average total number of species in all three combinations of the three regions (figure 17a). When compared with the species-accumulation curve in figure 16a, the T-S curve rose more steeply, it had higher $\mathrm{S} / \ln (\mathrm{x})$ ratio and thus a higher estimate of total species richness. Over $99 \%$ of the variability is explained when the T-S curve is fitted as a linear expression on a semi-log approximation, which may indicate that the assumption of a semi-log approximation to the curve is appropriate. The function of the T-S curve thus forms the basis for the subsequent extrapolation:
$163.44 * \ln (\mathrm{x})-109.44=\mathrm{y}$ (Equation 3; see figure 17b)

All samples consist of five pooled replicates; each covered a $0.1 \mathrm{~m}^{2}$ of the seabed. Thus each pooled sample consists of $0.5 \mathrm{~m}^{2}$, respectively. Therefore all the pooled samples, 55 in total, results in a $27.5 \mathrm{~m}^{2}$ total sampled area. Following the same assumption as in Ugland et al. (2003), it was assumed that each sample ( 5 pooled replicates) were representative of approximately $100 \mathrm{~m}^{2}$. The 55 samples were from three examined regions, which spanned over an area of roughly $11682 \mathrm{~km}^{2}\left(118620000 \mathrm{~m}^{2}\right)$. Assuming that one sample is representative of $100 \mathrm{~m}^{2}$, an extrapolation based on the coverage of the three areas results in:

Total no. of species $=163.44 * \ln (59310000)-109.44=2815$

Table 5 Summed recorded and estimated species richness in the Finnmark region IX.

| Area | Species <br> observed | Extrapolation of <br> species accumulation <br> curve | Chao2 | ICE | T-S curve |
| :---: | :---: | :---: | :---: | :---: | :---: |
| $116820000 \mathrm{~m}^{2}$ | 550 | 2164 | 734 | 683 | 2815 |

## 4 Discussion

Overall, the univariate indices depicted a species rich region. When the Finnmark region IX was compared to other survey areas along the Norwegian coast, the species richness was high (area 5 in Ellingsen et al. 2002, but all samples were not included in their article). As previously mentioned, species richness and abundance showed different patterns in the Finnmark region IX. The abundance was highest in the North- eastern area and the North-western area, and lowest in the South-western area (see figure 5b). However, the species richness was markedly higher in the South-western and North-western areas than in the North-eastern area (see figure 5a).

There was also most variability within the South-western area, as shown in the beta diversity analyses (see table 2, figure 8, figure A3.1 and table A3.1). Thus all the methods to examine beta diversity and the environmental variables gave the same results, except for the two dissimilarity measures biascorrected Jaccard and abundance-based Jaccard. The observed pattern in the latter dissimilarity measure is possibly due to higher and more variable abundance of species in the North-eastern and Northwestern areas (see figure 4b, 8b). When applying the bias-corrected Jaccard which accounts for unseen species in the samples, the resulting pattern was somewhat different. Here, the North-eastern area had the lowest variability, indicative of a more uniform species distribution pattern throughout this area when compared to the remainder areas (see figure 8c). However, the unbalanced study design could have been a driving factor behind the observed patterns. Whether this was the case, could not be resolved from regression modelling (see Results 3.3.1).

In concordance with the results from univariate analyses and the beta diversity analyses, the multivariate analyses based on the five main taxonomical groups also depicted considerable dissimilarity among samples in the Finnmark region IX (see figure 9). Low similarities within a dendrogram denote high beta diversity (Ellingsen \& Gray 2002). However, samples taken in the North-eastern were more similar and clustered together both for taxa and environmental variables (see figure 9), whereas the samples from the Western areas were more dissimilar and scattered in the cluster analysis. This also corresponds well with the findings in the univariate analyses. In the North-eastern area, primarily two groups were dominant in terms of abundance and numbers of the remainder groups were markedly lower in this area when compared to that in the other two areas (3.1, table 1). The outliers had higher
values of gravel and sand, in addition to higher temperature values (see figure 9 b ). The stress value in the NMDS-plot was high, 18.07, indicative of a great deal of heterogeneity in overall sample placement in a multidimensional space.

However, despite the variability in sample placement in a multidimensional space, the samples from the North-eastern area were clustered together which indicates a more homogeneous distribution, whereas the samples from the Western regions were scattered which in turn points to higher heterogeneity. Of the five dominant taxonomical groups, polychaetes are often numerically dominant in the benthic assemblages, both with regard to the number of species and their abundance (Olsgard et al. 2003). Polychaets was the most dominant group in the region Finnmark IX, which explains why this group was placed in the middle of the CA-plot (see figure 11). Fauchald (1984) suggested that the understanding of the distribution of recent polychaetes requires the analysis of ecological conditions rather than comparison of geographic ranges (Kupriyanova \& Badyaev 1998).

Thus polychaetes were influenced by all constraints in the CCA-ordination, but the environmental variable grain-size was particularly important for the distribution of polychaetes in sample 41 and 42 from the North-eastern area placed along the CC1-axis (see figure 12). As previously pointed out in the univariate analyses, polychaetes had very low values of Simpson's diversity in sample 41 and 44, explained by the dominance of Maldane sarsi and Lumbrinereis spp. in these two samples (see figure 7c, results 1.1). These two samples had among the highest values of grain-size recorded in samples. Average grain-size values were highest in the North-eastern area (see table A5). Polychaetes in the Maldanaidae family often live in sediments consisting of silt, and may dominate in bottom sediments with silt (Kirkegaard 1996). All the analyses indicate that the environmentally more homogenous North-eastern area had lower species richness with a predominance of more opportunistic species.

The direction of the vector shows the direction of the gradient, and the length of the arrow proportional to the correlation between the variable and the ordination axes (Oksanen 2008), hence sorting, temperature and longitude were important variables associated with the main ordination axis CCA1. In a multivariate analysis based on Bray-Curtis similarities, Ellingsen \& Gray (2002) found that faunal patterns were more closely related to sorting and depth than latitude. As shown in the CCA ordination plot (see figure 12), latitude was positively correlated with skewness. Both the North-eastern and the North-western areas had higher proportions of fine-skewed particles when compared to the South-western area (see table A5). Thus degree of skewness in the sediment increases with latitude. Sample placement showed that the number of mollusks were highest in samples with high values of skewness, namely the North-eastern area and in samples 50, 51 and 52 from the North-western area. As seen in figure 12, the environmental variables sorting and longitude associated with the ordination CCA2-axis are inverse, which means that when longitude increases towards East then values of sorting
decreases. Values of sorting were lowest in the North-eastern area when compared with the other areas, which indicate more homogenous sediments (see also table A5).

Overall, the benthic distribution pattern of the Finnmark region IX shown in the multivariate analyses were consistent with patterns found in the other analyses, the exponential of Shannon-Wiener diversity index resulted in less heterogeneity for the samples taken from the North-eastern area than from the samples taken in the two Western areas (see figure 6c). In addition, markedly lower temperature in this area also plays an important role for the benthic distribution patterns and may limit the distribution of more Southern species in the North-eastern area. Temperature also shared an inverse relationship with longitude in figure 14, positively correlated with sorting. Thus temperature decreases when longitude increases, e.g. towards the East in the Finnmark region IX.

Feeding guild characteristics were clearly associated with environmental gradients (see figure 13). The grainsize and TOM in sediment increased with depth, which were favorable conditions for polychaetes and sipunculids associated with these vectors. Increased organic content in the sediment at deeper waters may indicate less current and therefore more sedimentation, or be coupled up against how the primary production was distributed due to physical properties of the water masses. Sub-surface detrivores dominated in the North-eastern area, probably due to the high silt content in sediments, well suited for burrowing. In the detectability analysis, this area had the highest catchability of infaunal organisms (beta1) when compared to the other areas. The higher silt-clay content in this area probably favors infaunal organisms which may occur in high numbers. The South-western area had lower catchability for infaunal and immobile organisms than the North-eastern area, (beta1 and beta2).

Temperature and suspensivores were strongly positively correlated constraints, but that was probably because both variables increase in the same samples due to other factors, regardless of their mutual relationship (primarily in samples from the upper part of the South-western area). Temperature levels were highest in the South-western area (see figure A1), whereas the same samples also have a high proportion of suspensivores, probably due to higher levels of water transport and current (Ingvaldsen et al. 2004). In the North-western area, there was no difference in catchability between epibenthic and infaunal organisms. However, the North-western area had the highest proportion of mobile and epibenthic organisms when compared to the other areas. This is probably due to the environmental characteristics in the North-western area; there is more gravel and sand in this area in combination with higher values of sorting, which could indicate more current in this area compared with the other areas (see table A5). Within the Finnmark region IX, the North-western area has the most current due to high pulses of Atlantic water coming into the Barents Sea, northwards these water masses are displaced (Ingvaldsen et al. 2004).

Crustaceans were equally distributed among suspensivores, omnivores and carnivores, while echinoderms were mostly omnivores and some carnivores. Sorting and carnivore proportion are correlated, which may indicate that carnivore distribution is linked with more heterogeneous sediment characteristics. Not surprisingly, discretely mobile and mobile predominated also in the same samples, which seem plausible given the high numbers of carnivores in these samples (see figure 13). The vector for non-mobile organisms was positively correlated with depth and influential for sipunculids, a group consistent of non-mobile surface detrivores dependent on the percentage of TOM in the sediment.

In general, echinoderms were mobile omnivores; they decreased in numbers from the west towards the east in the Finnmark region IX, thus increasing in numbers with higher environmental heterogeneity. The North-eastern area was more environmentally homogenous than the two Western areas. Their presence in the North-western area was probably linked to higher environmental heterogeneity here. Echinoderms contributed to the detectability patterns found here, with the same likelihood of catching an epibenthic as an infaunal organism. However, representative sampling of echinoderms (especially brittle stars) is not feasible with a Van Veen grab, as these highly mobile organisms tend to move away from the pressure wave generated in front of the grab prior to sampling (Bjørn Gulliksen, pers.comm). Thus the chosen sampling gear was also a source of variation.

High abundance had highest effect on the catchability of organisms in the North-western area (see table 4). Higher abundance increased catchability of organisms in all the areas, but the effect was most pronounced in the North-western area and North-eastern area. This corresponds well with the interpolation of the abundance previously shown (univariate analyses, figure 5b), where the two Northern areas had the highest abundance of organisms. In addition, these findings probably also indicates that the numbers of sampling sites within each area affects the likelihood of an organism being sampled. In the North-western area, where the numbers of samples were lowest, the abundance of organisms had the biggest impact on whether or not an organism would be sampled. Whether the unbalanced study design affected the statistical inference between areas could not be determined in the beta diversity analysis, but it seems likely that this indeed was the case.

However, although considered species rich when compared to other examined soft-sediment areas along the Norwegian continental shelf, the Finnmark region IX had a similar distribution pattern of rare species as found along the whole Norwegian continental shelf. In concordance with the results found in Ellingsen et al. 2002, approximately $25 \%$ of the species were restricted to a single site (uniques) and $c .10 \%$ were restricted to only two sites (duplicates, $14 \%$ for the entire shelf). The nonparametric estimators of species richness such as Chao2 and ICE probably underestimated the total species richness. Chao-2 is predominantly a lower bound estimator for assemblages where rare species predominate (Colwell \& Coddington 1994). As shown by the reciprocal of Simpson's diversity measure
of dominance (figure 6c, figure 7c), the Finnmark region IX as a whole was not dominated by many rare species, with the exception of crustaceans in sample 27 and 29, and for all phyla in sample 23 and 30. The latter two samples are from the species-rich South-western area with the highest recorded species richness. On the other hand, the extrapolation from the semi-log approximation of the T-S curve overestimated the total species richness, 2815 species for the Snow white monitoring area was excessive; as it is approximately five times the recorded species. This was possibly because the estimates are adjusted upwards to account for beta-diversity when this diversity was already captured in the sampling design (O'Dea et al. 2006).

The estimates in the detectability analysis were also measures of the species richness in the areas. In summary, the biggest area with the most samples, South-western, had the highest amount of variability (s.e.) and the highest estimated species richness (see table A2.1), followed by the same pattern in the intermediate North-eastern area (see table A2.4) and then in the smallest North-western area (see table A2.6). These results coincide with the remainder detectability analysis, as seen in table 4 higher abundance increased catchability in the North-eastern and North-western area. However, it was difficult to separate whether the pattern was driven by generally higher abundance in these two areas or if the lower number of samples here affected the cathability (likelihood of being sampled).

The differing species richness and varying detectability were also a considerable source of variation among the three examined areas. To obtain correct measures of the likely total species richness proved difficult, as the applied methodologies all had weaknesses and limitations. The ICE and Shao2 most likely underestimated the total species richness, whereas the TS-curve overestimated the total number of species present in the three areas. By extrapolating beyond the data set, one can identify where the species accumulation curve reaches an asymptote and get an estimate of how many samples is required to capture the probable total species richness at the time of sampling, which could prove useful when monitoring an area. One never gets all the samples - the only relevant aspect is the variance and the bias which will decrease with increasing sample size (Nigel Yoccoz, pers.comm.). But the estimate of the TS-curve is provided that the same relationship of area sampled and species richness will hold when extrapolated to a bigger area, in addition to implying that there is correct division of areas into spatial subsets based on environmental heterogeneity (O'Dea et al. 2006), often this is not the case.

However, although the claim that there is twice as many species along the Norwegian coastline is an extrapolation (Ugland et al. 2003), it indicates something important; namely that the total species richness is probably much higher than recorded. Consequently, previous studies may have had high sampling error, too few samples and insufficient detectability of organisms. Failure to detect all species in sampled communities not only leads to estimates of species richness that are negatively biased but also produces biased estimates of the comparative or relative richness of two (or more) areas. In
addition, the use of count statistics as naïve estimates leads to problems estimating quantities reflecting differences in community composition (Nichols et al. 1998). If we are to base our conclusions on objective criteria (e.g. by the use of statistical models), we can only allow ourselves to make inferences about the statistical population being sampled (Ims \& Yoccoz 2006).

In summary, the benthic fauna in the Finnmark region IX is subjected to several sources of variation on different scales, which in sum all add bias to the statistical inference in the monitoring programme. So basically the sources of variation on benthic marine fauna are numerous, confounded and exist on different scales. In addition, the fact that all the three examined areas were both temporally and spatially heterogeneous and unevenly affected by various anthropogenic factors adds to the complexity of the monitored system. The available resources to monitor these benthic patterns are limited, and the causal mechanisms behind these observed patterns difficult to entangle. But if we return to the main focus in the "how, what and why monitor" article by Yoccoz et al. (2001), could there be a solution for how to improve future monitoring programmes in the region without exceeding costs notably? But first, what are the strongholds and weaknesses in the current study design?

The current study design has some strongholds. Firstly, the sampling was carried out during approximately the same short time period of the year both in 1998 and 2000, which efficiently minimizes potential bias from annual variation in the benthic communities when comparing differences between years. A final requirement of the sampling protocol is that the entire survey must be completed within a sufficiently short time that local extinctions or colonization cannot change the composition of species that occupy a sample location (Dorazio et al. 2006). Five replicates were taken per sample, thus the variance within each sample could be examined and the effect of small-scale variation reduced. The mapping of the average biodiversity along the Norwegian continental shelf based on data from the OLF-database, resulted in several articles which increased the knowledge of large-scale biodiversity pattern along the shelf, and the correlation of benthic fauna with environmental variability (Ellingsen 2001; Ellingsen \& Gray 2002; Ellingsen 2002). Hence, this mapping of the sea bed resulted in knowledge of biodiversity patterns both in the region Finnmark IX and along the Norwegian coast, but failure to among other address the two major pitfalls in monitoring programmes, e.g. detection error and spatial variation rendered the resulting data material unsuited for monitoring purposes. The severely unbalanced study design meant that it was not possible to conclude whether the numbers of samples in each area was the driving force behind observed benthic pattern.

As shown in the detectability analyses, the fewer samples in an area, the more important was abundance for the probability to be detected. Failure to sample the same sites on at least two occasions means that the stochastically variation occurring in samples was unknown. Thus it is not possible to deduce whether species were not sampled both years in the area either because they were not present at a
location, or due to the fact that these organisms were present but not detected. "The purpose of temporal replication at each sample location is to provide the information needed to estimate the probability of detecting each species, (given that it is present separately from its probability of occurrence, a minimum of two visits is needed at each sample location)" (Dorazio et al. 2006). If the natural variability in a marine system is not known prior to anthropogenic activities, separating the effects of various confounded variables a posteriori is virtually impossible.

Consequently, the need for a developing a robust sampling design apriori of sampling which accounts for temporal and spatial variation; and which includes enough samples to give a reasonable estimate for the total species richness, cannot be stressed enough. In order to design an adequate conservation strategy to meet the increasing challenges of tomorrow, we need to define which monitoring questions need answers prior to sampling. Future studies need a rigorous approach starting with clearly defined monitoring questions and a study design combining adequate sampling effort with appropriate spatial sampling unit allocation. Failure to adhere to a controlled sampling design will lead to a situation in which the study design is unable to answer even simple questions about changes that are taking place. This is especially important in a complex marine ecosystem where numerous feedbacks and interactions make it difficult to pinpoint causal mechanisms giving rise to observed changes. To obtain measurements of the natural variation in marine systems is increasingly import for several reasons. Knowledge of naturally occurring temporal variation is necessary in a process where the aim is to separate the effects of local predictor variables and anthropogenic factors.

By upholding the recommendation by SFT of sample allocation in a cross formation adjacent to an oil or gas installation, the variation stemming from other sources than the oil or gas excavation would decrease. Spreading the sample intensity over such a large scale as today decreases the detectability and increases spatial variation. By reducing the scale, the statistical inference is improved. Since sampling is routinely imposed to take place on three different occasions, the same sites along the crosses could be sampled on several times, which would provide us with a measure of detectability and temporal variation. The chances of detecting long-term chronic effects from oil or gas excavation would increase, and therefore also the likelihood of developing new business practices to remedy adverse effects on the adjacent environment. In turn, the oil industry may gain access to areas currently closed for drilling due to uncertainties regarding the effects of oil and gas excavation on the immediate surroundings. In addition, there would be a higher likelihood of separating potential negative environmental effects of the oil industry from that of the king crab invasion or bottom trawling, due to the increased statistical inference. An ongoing problem is the fact that the exact locations of oil installations are not known on beforehand. However, it was the experience of John Gray, a renowned expert in the field of benthic monitoring, that adverse environmental affects were restricted to a circle of 300 m around the
installation (Gray 1999). Thus when the approximate placement of the installation is known, a possible solution is to allocate an excavation area of a given percentage of $\mathrm{x} \mathrm{km}{ }^{2}\left(3^{2} \mathrm{~km} * 3.14=\mathrm{x}\right)$, and thereafter place the installation within this parameter and place the cross from this circle. That would have been preferable to placing the site in a grid formation along longitudes and latitudes (Bakke et al. 2000).

Secondly, by implementing estimates of natural variation into models, we may model the effects of both natural and anthropogenic variables on biodiversity and possibly identify causal mechanisms. Such models may also show us what the future will look like given a certain outcome, for instance the effects an uncontrollable growth in the king crab population will have on the benthic fauna in a given area or an oil spill. This opens up for an informed decision making process based on actual facts and a sustainable development, where conservation of biodiversity is balanced towards much needed business life along the coast.

## Acknowledgments

This project would never have seen the light of day without my thesis advisors; Kari Ellingsen, Nigel Yoccoz, Per Fauchald and Bjørn Gulliksen, to whom I am eternally grateful. Thank you for sharing your vast experience and professional knowledge with me. Thanks to Bård-Jørgen Bårdsen, Gunnhild Garte Nervold and Torkild Tveraa for helpful discussions in statistics and R.

I'm also eternally grateful to Morten Johansen for your love and support, my love and the incarnation of everything good in this world. I'm grateful for the patience and support of friends and family, especially my sister Sølvi Bersås for professional and diligent referee work, my brother Oddbjørn Bersås for computer backup in map software and my parents for their unfailing belief in me and support.

A big thank you to Harald Loeng (Physical oceanographer) at The Marine Research Institute in Bergen (IMR) for useful information on how to obtain CTD data for a given area and time period, Randi B. Ingvaldsen (Physical oceanographer) and Helge Sagen (technician) for information on physical properties in the Western Barents Sea and Oystein Ostensen (senior engineer) for CTD data, in addition to the friendly and helpful staff at IMR's information desk.

Thanks to Ketil Dahl at Olex for permission to use one of your test-machines to run Olex software version 7.1, in order to get a realistic view of the seafloor topography in the Snow White monitoring area.

Thanks to Ivar Rødum at Tromsø Maritime skole for granting me access and use of their mapping program Telchart V version 1,47B \#5062-2.4 CMAP \#5136, in order to make the sea maps in this thesis.

Thanks to the knowledgeable and friendly staff at the University Museum library for helping out in the search of adequate literature to build up my databases on functional groups and biogeographical distribution; Liv-Inger Olsen and Magne. Thanks to Robert Andre Johansen at Marbank for helpful suggestions on bristle worms literature for the Functional Groups database, benthic oracle and the best boss ever! Thanks to Irina Malyutina for helpful insight on feeding habits of deep-water isopods.

## 5 References

Aitken, A.E. \& Gilbert, R. (1996) Marine mollusca from expedition Fiord, western Axel Heiberg Island, Northwest Territories, Canada. Arctic, 49, 29-43.

Allen, J.A. (2000) An unusual suctorial montacutid bivalve from the deep Atlantic. Journal of the Marine Biological Association of the United Kingdom, 80, 827-834.

Anderson, M.J. (2006) Distance-based tests for homogeneity of multivariate dispersions. Biometrics, 62, 245-253.

Anderson, M.J., Ellingsen, K.E. \& McArdle, B.H. (2006) Multivariate dispersion as a measure of beta diversity. Ecology Letters, 9, 683-693.

Austin, M.P. (1976) On non-linear species response models in ordination. Plant Ecology, 33, 33-41.
Bakke, S., Gjøs, N., Oreld, F., Møskeland, T., Faksness, L.G. \& Nøland, S.A. (1999) Monitoring survey in region IX - Finnmark in 1998.

Bakke, S., Gjøs, N., Oreld, F., Møskeland, T., Faksness, L.G. \& Nøland, S.A. (2001) Monitoring survey in region IX - Finnmark in 2000.

Biernbaum, C.K. (1979) Influence of sedimentary factors on the distribution of benthic amphipods of Fishers Island Sound, Connecticut. Journal of Experimental Marine Biology and Ecology, 38, 201-223.

Brandt, A. \& Berge, J. (2007) Peracarid composition, diversity and species richness in the area of the Northeast Water polynya, East Greenland (Crustacea, Malacostraca). Polar Biology, 31, 15-22.

Brandt, A., Brökeland, W., Brix, S. \& Malyutina, M. (2004) Diversity of Southern Ocean deep-sea Isopoda (Crustacea, Malacostraca) - a comparison with shelf data. Deep-Sea Research Part II, 51, 17531768.

Brenke, N. (2002) The benthic community of the Great Meteor Bank. Oceanography and ecology of seamounts: indicators of unique ecosystems. Selected papers from the ICES Annual Science Conference 2002, ICES, CM 2002 / M:30, Copenhagen, 1-12.

Buchanan, J.B. (1963) The bottom fauna communities and their sediment relationships off the coast of Northumberland. Oikos, 14, 154-175.

Buhl-Mortensen, L. (1996) Amphipod fauna along an offshore-fjord gradient. Journal of Natural History, 30, 23-49.

Buhl-Mortensen, L. \& Mortensen, P.B. (2004) Crustaceans associated with the deep-water gorgonian corals Paragorgia arborea (L., 1758) and Primnoa resedaeformis (Gunn., 1763). Journal of Natural History, 38, 1233-1247.

Buhl-Mortensen, L. \& Mortensen, P.B. (2005) Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In: Cold-W ater Corals and Ecosystems (eds. Freiwald, A. \& Roberts, J.M.), pp. 849-879, Springer-Verlag, Berlin Heidelberg.

Cartes, J.E., Huguet, C., Parra, S. \& Sanchez, F. (2007) Trophic relationships in deep-water decapods of Le Danois bank (Cantabrian Sea, NE Atlantic): Trends related with depth and seasonal changes in food quality and availability. Deep-Sea Research Part I, 54, 1091-1110.

Chao, A. \& Yang, H.C. (2003) Program CARE-2 (for Capture-Recapture Part. 2).
bttp:/ / chao.stat.nthu.edu.tw/ softwareCE.html.
Chao, A. \& Yang, H.C. (2006) User guide for Program CARE-2.
http:/ / chao.stat.nthu.edu.tw/UserGuide_care-2.pdf.
Chevrier, A., Brunel, P. \& Wildish, D.J. (1991) Structure of a suprabenthic shelf sub-community of gammaridean Amphipoda in the Bay of Fundy compared with similar subcommunities in the Gulf of St-Lawrence. Hydrobiologia, 223, 81-104.

Colwell, R.K. (2006) EstimateS: Statistical estimation of species richness and shared species from samples, version 8.0. http:/ / viceroy.eeb.uconn.edu/ estimates.

Colwell, R.K. \& Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 345, 101-118.

Crawford, G.I. (1937) Notes on the distribution of burrowing Isopoda and Amphipoda in various soils on the sea bottom near Plymouth. Journal of the Marine Biological Association of the United Kingdom, 21, 631646.

Dayton, P.K., Sala, E., Tegner, M.J. \& Thrush, S. (2000) Marine reserves: parks, baselines, and fishery enhancement. Bulletin of Marine Science, 66, 617-634.

De Broyer, C., Nyssen, F. \& Dauby, P. (2004) The crustacean scavenger guild in Antarctic shelf, bathyal and abyssal communities. Deep-Sea Research Part II, 51, 1733-1752.

Denisenko, S.G., Cochrane, S., Denisenko, N.V. \& Dahle, S. (2008) Biogeographic boundary and zoobenthos in the Barents sea. Presentation, Arctic Frontiers, Tromsø, Norway.

Dixon, I.M.T. \& Moore, P.G. (1997) A comparative study on the tubes and feeding behaviour of eight species of corophioid Amphipoda and their bearing on phylogenetic relationships within the Corophioidea. Pbilosophical Transactions of the Royal Society of London Series B-Biological Sciences, 352, 93-112.

Dorazio, R.M. \& Jelks, H.L. (2005) Improving removal-based estimates of abundance by sampling a population of spatially distinct subpopulations. Biometrics, 61, 1093-1101.

Dorazio, R.M., Royle, J.A., Söderström, B. \& Glimskär, A. (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology, 87, 842-854.

Dziaduch, D. (2007) A new occurrence of the benthic amphipod Dyopedos monacanthus (Metzger, 1875) in the southern Baltic Sea - the first record in the Slupsk Furrow. Oceanologia, 49, 439-445.

Ellingsen, K.E. (2001) Biodiversity of a continental shelf soft-sediment macrobenthos community. Marine Ecology Progress Series, 218, 1-15.

Ellingsen, K.E. (2002) Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. Marine Ecology Progress Series, 232, 15-27.

Ellingsen, K.E. \& Gray, J.S. (2002) Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf? Journal of Animal Ecology, 71, 373-389.

Enckell, P.H. (1998) Kräftdjur. Graphic Publishing, Odense.
Enequist, P. (1949) Studies on the soft-bottom amphipods of the Skagerak. Zoologiska bidrag fran Uppsala, 28, 297-492.

Fauchald, K. \& Jumars, P.A. (1979) The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biology, Annual Reviem, 17, 193-284.

Fauchald, K. \& Rouse, G. (1997) Polychaete systematics: past and present. Zoologica Scripta, 26, 71-138.
Gibson, R., Hextall, B. \& Rogers, A. (2001) Photographic Guide to the Sea and Shore Life of Britain and NorthWest Europe. Oxford University Press, Oxford.

González-Macías, C., Schifter, I., Lluch-Cota, D., Méndez-Rodriguez, L. \& Hernández-Vázquez, S. (2009) Assessment of benthic changes during 20 years of monitoring the Mexican Salina Cruz Bay. Environmental Monitoring and Assessment, 149, 113-132.

Gray, J.S. (1997) Gradients in marine biodiversity. In: Marine Biodiversity. Patterns and Processes (eds. Ormond, R.F.G., Gage, J.D. \& Angel, M.V.), pp. 18-34, Cambridge University Press, Cambridge.

Gray, J.S. (2000) The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. Journal of Experimental Marine Biology and Ecology, 250, 23-49.

Gray, J.S., Bakke, T., Beck, H.J. \& Nilssen, I. (1999) Managing the environmental effects of the Norwegian oil and gas industry: from conflict to consensus. Marine Pollution Bulletin, 38, 525-530.

Harper, E.M., Palmer, T.J. \& Hudson, J.D. (2002) The Middle Jurassic bivalve 'Cuspidaria' ibbetsoni: a corbulid not a septibranch. Palaeontology, 45, 759-769.

Hayward, P.J. \& Ryland, J.S. (1990) The Marine Fauna of the British Isles and North-West Europe. Volume 1. Introduction and Protozoans to Arthropods. Clarendon Press, Oxford.

Heger, A., King, N.J., Wigham, B.D., Jamieson, A.J., Bagley, P.M., Allan, L., Pfannkuche, O. \& Priede, I.G. (2007) Benthic bioluminescence in the bathyal North East Atlantic: luminescent responses of Vargula norvegica (Ostracoda: Myodocopida) to predation by the deep-water eel (Synaphobranchus kaupii). Marine Biology, 151, 1471-1478.

Herbert, D.G. (1991) Foraminiferivory in a Puncturella (Gastropoda - Fissurellidae). Journal of Molluscan Studies, 57, 127-140.

Hessler, R.R. \& Strömberg, J.-O. (1989) Behavior of janiroidean Isopods (Asellota), with special reference to deep-sea genera. Sarsia, 74, 145-159.

Hessler, R.R. \& Thistle, D. (1975) Place of origin of deep-sea isopods. Marine Biology, 32, 155-165.
Holte, B. (1998) The macrofauna and main functional interactions in the sill basin sediments of the pristine Holandsfjord, Northern Norway, with autecological reviews for some key-species. Sarsia, 83, 55-68.

Hop, H., Pearson, T., Hegseth, E.N., Kovacs, K.M., Wiencke, C., Kwasniewski, S., Eiane, K., Mehlum, F., Gulliksen, B., Wlodarska-Kowalczuk, M., Lydersen, C., Weslawski, J.M., Cochrane, S., Gabrielsen, G.W., Leakey, R.J.G., Lonne, O.J., Zajaczkowski, M., Falk-Petersen, S., Kendall, M., Wangberg, S.A., Bischof, K., Voronkov, A.Y., Kovaltchouk, N.A., Wiktor, J., Poltermann, M., di Prisco, G., Papucci, C. \& Gerland, S. (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Research, 21, 167-208.

Hult, J. (1941) On the soft-bottom Isopods of the Skager Rak. Zoologiska bidrag frain Uppsala, 21, 1-234.
Hwang, W.H. \& Chao, A. (2002) Continuous-time capture-recapture models with covariates. Statistica Sinica, 12, 1115-1131.

Ims, R. \& Yoccoz, N.G. (2006) Ecological Methods - Study Design and Statistical Analysis. Institute of biology, Faculty of science, University of Tromsø, Tromsø.

Ingvaldsen, R., Loeng, H. \& Asplin, L. (2002) Variability in the Atlantic inflow to the Barents Sea based on a one-year time series from moored current meters. Continental Shelf Research, 22, 505-519.

Ingvaldsen, R.B.R., Asplin, L. \& Loeng, H. (2004) The seasonal cycle in the Atlantic transport to the Barents Sea during the years 1997-2001. Continental Shelf Research, 24, 1015-1032.

Karas, P., Gorny, M. \& Alarcón-Muñoz, R. (2007) Experimental studies on the feeding ecology of Munida subrugosa (White, 1847) (Decapoda: Anomura: Galatheidae) from the Magellan region, southern Chile. Scientia Marina, 71, 187-190.

Keable, S.J. (1995) Structure of the marine invertebrate scavenging guild of a tropical reef ecosystem field studies at Lizard Island, Queensland, Australia. Journal of Natural History, 29, 27-45.

Kirkegaard, J.B. (1992) Havborsteorme. I. Errantia. Dansk Naturhistorisk Forening, København.
Kirkegaard, J.B. (1996) Havborsteorme. II. Sedentaria. Dansk Naturhistorisk Forening, København.
Klages, M., Vopel, K., Bluhm, H., Brey, T., Soltwedel, T. \& Arntz, W.E. (2001) Deep-sea food falls: first observation of a natural event in the Arctic Ocean. Polar Biology, 24, 292-295.

Klitgaard, A.B. (1995) The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, Northeastern Atlantic. Sarsia, 80, 1-22.

Koleff, P., Gaston, K.J. \& Lennon, J.J. (2003) Measuring beta diversity for presence-absence data. Journal of Animal Ecology, 72, 367-382.

Koukouras, A., Russo, A., Voultsiadou-Koukoura, E., Arvanitidis, C. \& Stefanidou, D. (1996)
Macrofauna associated with sponge species of different morphology. Marine Ecology, 17, 569-582.
Krapp-Schickel, G. (1993) Do algal-dwelling amphipods react to the 'critical zones' of a coastal slope? Journal of Natural History, 27, 883-900.

Krapp-Schickel, T. (2005) Cressidae (Crustacea: Amphipoda) collected by the BIOFAR and BIOICE programmes near the Faroes and Iceland (N-Atlantic). BIOFAR Proceedings, 2005, 150-166.

Kupriyanova, E.K. \& Badyaev, A.V. (1998) Ecological correlates of Arctic Serpulidae (Annelida, Polychaeta) distributions. Ophelia, 49, 181-193.

Kuris, A.M., Blau, S.F., Paul, A.J., Shields, J.D. \& Wickham, D.E. (1991) Infestation by brood symbionts and their impact on egg mortality of the red king crab, Paralithodes camtschatica, in Alaska: geographic and temporal variation. Canadian Journal of Fisheries and Aquatic Sciences, 48, 559-568.

Lee, C.N. \& Morton, B. (2005) Demography of Nebalia sp. (Crustacea: Leptostraca) determined by carrion bait trapping in Lobster Bay, Cape d'Aguilar Marine Reserve, Hong Kong. Marine Biology, 148, 149-157.

Legendre, P. \& Legendre, L. (1998) Numerical Ecology. Elsevier Science, Amsterdam.
Levin, S.A. (1992) The problem of pattern and scale in ecology. Ecology, 73, 1943-1967.
Lindal Jørgensen, L. (2005) Impact scenario for an introduced decapod on Arctic epibenthic communitites. Biological Invasions, 7, 949-957.

Maddocks, R.F. (1977) Zoogeography of macrocyprididae (Ostracoda). In: Aspects of Ecology and Zoogeography of Recent and Fossil Ostracoda (eds. Löffler, H. \& Danielopol, D.), pp. 147-157, Kluwer Academic Publishers, The Hague.

Magurran, A.E. (2004) Measuring Biological Diversity. Blackwell Publishing, Malden, Massachusetts.
Mao, C.X. \& Colwell, R.K. (2005) Estimation of species richness: mixture models, the role of rare species, and inferential challenges. Ecology, 86, 1143-1153.

Massin, C. (1982) Food and feeding mechanisms: Holothuroidea. In: Echinoderm Nutrition (eds. Jangoux, M. \& Lawrence, J.M.), pp. 43-55, A.A.Balkema, Rotterdam.

Maynou, F. \& Cartes, J.E. (1998) Daily ration estimates and comparative study of food consumption in nine species of deep-water decapod crustaceans of the NW Mediterranean. Marine Ecology Progress Series, 171, 221-231.

Miskov-Nodland, K., Buhl-Mortensen, L. \& Høisæter, T. (1999) Has the fauna in the deeper parts of the Skagerrak changed? A comparison of the present amphipod fauna with observations from 1933/37. Sarsia, 84, 137-155.

Moen, F.E. \& Svendsen, E. (2004) Dyreliv i Havet - Nordeuropeisk Marin Fauna. Kom Forlag, Kristiansund.

Mortensen, T. (1927) Handbook of the Echinoderms of the British Isles. Oxford University Press, London.
Nichols, J.D., Boulinier, T., Hines, J.E., Pollock, K.H. \& Sauer, J.R. (1998) Inference methods for spatial variation in species richness and community composition when not all species are detected. Conservation Biology, 12, 1390-1398.

O'Dea, N., Whittaker, R.J. \& Ugland, K.I. (2006) Using spatial heterogeneity to extrapolate species richness: a new method tested on Ecuadorian cloud forest birds. Journal of Applied Ecology, 43, 189-198.

Oksanen, J. (2008) VEGAN: An introduction to ordination. bttp:// cran.r-
project.org/web/packages/vegan/vignettes/intro-vegan.pdf.
Olabarria, C. \& Thurston, M.H. (2003) Latitudinal and bathymetric trends in body size of the deep-sea gastropod Troschelia berniciensis (King). Marine Biology, 143, 723-730.

Oliver, G. \& Allen, J.A. (1980) The functional and adaptive morphology of the deep-sea species of the Arcacea (Mollusca, Bivalvia) from the Atlantic. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 291, 6-76.

Oliver, G. \& Holmes, A.M. (2006) The Arcoidea (Mollusca: Bivalvia): a review of the current pheneticbased systematics. Zoological Journal of the Linnean Society, 148, 237-251.

Olsgard, F., Brattegard, T. \& Holthe, T. (2003) Polychaetes as surrogates for marine biodiversity: lower taxonomic resolution and indicator groups. Biodiversity and Conservation, 12, 1033-1049.

Padilla, D.K. (1985) Structural resistance of algae to herbivores. Marine Biology, 90, 103-109.
Parker, A.R. (2000) The coelotrich: form and function of an unusual sensillum in Lowrya (Ostracoda: Myodocopina: Cypridinidae). Pbilosophical Transactions of the Royal Society of London Series B-Biological Sciences, 355, 1121-1124.

R Development Team. (2009) R: A language and environment for statistical computing. bttp:/ / www.Rproject.org.

Rowe, G.T., Boland, G.S., Escobar Briones, E.G., Cruz-Kaegi, M.E., Newton, A., Piepenburg, D., Walsh, I. \& Deming, J. (1997) Sediment community biomass and respiration in the Northeast water polynya, Greenland: a numerical simulation of benthic lander and spade core data. Journal of Marine Systems, 10, 497-515.

Schaffner, L.C. \& Boesch, D.F. (1982) Spatial and temporal resource use by dominant benthic Amphipoda (Ampeliscidae and Corophiidae) on the Middle Atlantic Bight Outer Continental-Shelf. Marine Ecology Progress Series, 9, 231-243.

Schnabel, K.E. \& Hebert, P.D.N. (2003) Resource-associated divergence in the Arctic marine amphipod Paramphithoe hystrix. Marine Biology, 143, 851-857.

Sheridan, P. (1997) Benthos of adjacent mangrove, seagrass and non-vegetated habitats in Rookery Bay, Florida, USA. Estuarine, Coastal and Shelf Science, 44, 455-469.

Steele, D.H. \& Steele, V.H. (1993) Biting mechanism of the amphipod Anonyx (Crustacea: Amphipoda: Lysianassoidea). Journal of Natural History, 27, 851-860.

Stransky, B. (2007) Abundance, diversity and species composition of the Peracardia (Crustacea: Malacostraca) from the South Greenland shelf. Ph. D. thesis, University of Hamburg, Department of biology, Faculty of Mathematics, Informatics and Science.

Stransky, B. \& Svavarsson, J. (2006) Astacilla boreaphilis sp nov (Crustacea : Isopoda : Valvifera) from shallow and deep North Atlantic waters. Zootaxa, 1-23.

Svavarsson, J. \& Ólafsdóttir, S.H. (1999) Foraminiferan (Protozoa) epizoites on the anthuridean (Crustacea, Isopoda) Calathura brachiata (Stimpson). Journal of Natural History, 33, 1423-1432.

Taylor, J.D. \& Taylor, C.N. (1977) Latitudinal distribution of predatory gastropods on eastern Atlantic shelf. Journal of Biogeography, 4, 73-81.

Thiel, M. (1999) Host-use and population demographics of the ascidian-dwelling amphipod Leucothoe spinicarpa: indication for extended parental care and advanced social behaviour. Journal of Natural History, 33, 193-206.

Todd, J.A. (2001) NMITA Molluscan Life Habits databases. bttp:// eusmilia.geology. uiowa.edu/ database/ mollusc/ mollusclifestyles. btm.

Tyler, P.A., Emson, R.H., Sumida, P. \& Howell, K. (2005) Ophiuroid distribution at sublittoral and bathyal depths round the Faroe Islands, NE Atlantic Ocean. BIOFAR Proceedings, 2005, 175-194.

Ugland, K.I., Gray, J.S. \& Ellingsen, K.E. (2003) The species-accumulation curve and estimation of species richness. Journal of Animal Ecology, 72, 888-897.

Vader, W. \& Krapp-Schickel, G. (1996) Redescription and biology of Stenothoe brevicornis Sars (Amphipoda: Crustacea), an obligate associate of the sea anemone Actinostola callosa (Verrill). Journal of Natural History, 30, 51-66.

Valentine, J.W., Roy, K. \& Jablonski, D. (2002) Carnivore/non-carnivore ratios in northeastern Pacific marine gastropods. Marine Ecology Progress Series, 228, 153-163.
von Quillfeldt, C.H. \& Dommasnes, A. (2005) Indikatorer og miljøkvalitetsmål for Barentshavet., Institute for Marine Research and Norwegian Polar Institute.

Warner, G. (1982) Food and feeding mechanims: Ophiuroidea. In: Echinoderm Nutrition (eds. Jangoux, M. \& Lawrence, J.M.), pp. 161-180, A.A.Balkema, Rotterdam.

Weslawski, J.M., Wlodarska-Kowalczuk, M. \& Legezynska, J. (2003) Occurence of soft bottom macrofauna along the depth gradient in High Arctic, $79^{\circ}$ N. Polish Polar Research, 24, 73-88.

Wetzer, R., Brusca, R.C. \& Wilson, G.D.F. (1997) The order Isopoda. In: Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 11-The Crustacea Part 2 (eds. Blake, J.A. \& Scott, P.H.), pp. 1-120, Santa Barbara Museum of Natural History, Santa Barbara, California.

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs, 30, 279-338.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. Taxon, 21, 213-251.
Wilson, G.D.F. \& Hessler, R.R. (1987) Speciation in the deep-sea. Annual Review of Ecology and Systematics, 18, 185-207.

Wolff, T. (1962) The systematics and biology of bathyal and abyssal Isopoda Asellota. Galathea Report, 6, Danish Science Press, Ltd, Copenhagen, 1-320.

Yoccoz, N.G., Nichols, J.D. \& Boulinier, T. (2001) Monitoring of biological diversity in space and time. Trends in Ecology \& Evolution, 16, 446-453.

## 6 Appendix

### 6.1 Lab analyses and environmental variables

## Sediment analysis

$\Phi$ (Phi)
$\Phi$ (phi) refers to sediment particle size in terms of sieve mesh size necessary to retain a particular size fraction. Formula: $\Phi=-\log _{2}$ (sieve mesh in millimetres)

Median grain size
This is a measure of central tendency. Commonly used is the median phi value, $\Phi_{50}$, which is the value of $\Phi$ corresponding to $50 \%$ of the cumulative frequency. The interpretation of median grain size is shown in Table A1.

Table A1: The interpretation of median grain size values.

| Median grain size $\left(\Phi_{50}\right)$ | Sediment type |
| :--- | :--- |
| $<-1$ | Granule/pebble |
| $-1-0$ | Very coarse sand |
| $0-1$ | Coarse sand |
| $1-2$ | Medium sand |
| $2-3$ | Fine sand |
| $3-3.75$ | Muddy sand |
| $3.75-5$ | Coarse silt |
| $5-6$ | Medium silt |
| $6-8$ | Fine silt |
| $>8$ | Clay |

Sorting
This is a measure of degree of scatter, providing info on the uniformity or homogeneity of the sediment. This is given by the formula:
$\sigma_{\mathrm{I}}=\left(\Phi_{84^{-}}-\Phi_{16}\right) / 4+\left(\Phi_{95^{-}} \Phi_{5}\right) / 6.6$
where for example $\Phi_{84}$ is the 84 percentile of $\Phi$. Interpretation of $\sigma_{\mathrm{I}}$ is provided in Table 2.
Table A2: The interpretation of sorting $\left(\sigma_{\mathrm{I}}\right)$ values.

| $\sigma_{\mathrm{I}}$ | Degree of sorting |
| :--- | :--- |
| $<0.35$ | Very well sorted |
| $0.35-0.50$ | Well sorted |
| $0.50-0.71$ | Moderately well sorted |
| $0.71-1.00$ | Moderately sorted |
| $1.00-2.00$ | Poorly sorted |
| $2.00-4.00$ | Very poorly sorted |
| $>4.00$ | Extremely poorly sorted |

## Skewness

This is a measure of degree of symmetry and assesses the predominance of particular sediment fractions as a departure from a normal distribution. Formula:
$\mathrm{Sk}_{\mathrm{I}}=\left(\Phi_{16}+\Phi_{84}-2 \Phi_{50}\right) /\left(2\left(\Phi_{84}-\Phi_{16}\right)\right)+\left(\Phi_{5}+\Phi_{95}-2 \Phi_{50}\right) /\left(2\left(\Phi_{95}-\Phi_{5}\right)\right)$
Interpretation of skewness values are provided in Table 3.
Table A3: The interpretation of skewness ( $\mathrm{Sk}_{\mathrm{I}}$ ) values.

| $\mathrm{Sk}_{\mathrm{I}}$ | Skewness |
| :--- | :--- |
| -1.00 to -0.30 | Strongly skewed towards coarse particles |
| -0.30 to -0.10 | Coarse skewed |
| -0.10 to 0.10 | Symmetrical |
| 0.10 to 0.30 | Fine skewed |
| 0.30 to 1.00 | Strongly skewed towards fine particles |

Kurtosis
Kurtosis provides an assessment of the frequency distribution of particle sizes, and gives information about the range of particle sizes in the sample. An excessively peaked distribution is called leptokurtic, while a flattened distribution is called platykurtic. Formula:
$\mathrm{K}_{\mathrm{G}}=\left(\Phi_{90}-\Phi_{5}\right) /\left(2.44\left(\Phi_{75}-\Phi_{25}\right)\right)$
Interpretation of kurtosis values are provided in Table 4.
Table A4: The interpretation of kurtosis $\left(\mathrm{K}_{\mathrm{G}}\right)$ values.

| $\mathrm{K}_{\mathrm{G}}$ | Kurtosis |
| :--- | :--- |
| $<0.67$ | Very platykurtic |
| $0.67-0.90$ | Platykurtic |
| $0.90-1.11$ | Mesokurtic (nearly normal) |
| $1.11-1.50$ | Leptokurtic |
| $>1.50$ | Very leptokurtic |

## List A1: Taxa removed prior to data analysis

## Taxa higher than species/genus level removed prior to data analysis:

Amparetidae sp., Amphipoda spp., Anthozoa sp., Anthuridae sp., Archiannelida spp., Ascidiacea spp., Asteroida spp., Brachyura spp., Calliopiidae spp., Caudofoveata spp., Decapoda sp., Flabelliseridae spp., Holothuroidea spp., Hydrozoa sp., Isopoda spp., Nemertea spp., Oligochaeta sp., Oligochaeta spp., Pogonophora spp., Polychaeta spp., Pycnogonidae sp., Sabellidae sp., Serpulidae sp., Sipuncula spp., Sphaerodoridae spp., Tanaidacea spp., Thyasiridae spp. and Tunicata spp.

Species pooled together (one species (sp.) and many species (spp.) from a genus were pooled together and included as one species in analyses):

- Ampelisca sp. and $A m p e l i s c a$ spp. now listed as $A$.spp. (1998)
- Ophiura sp. and Ophiura spp. now listed as O.spp. (1998)
- Diastylis sp. and Diastylis spp, now listed as D.spp. (2000)
- Ampelisca sp. and Ampelisca spp., now listed as $A$.spp. (1998\&2000)
- Diastylis sp. and Diastylis sp., now listed as D.spp. (1998\&2000)
- Eusyllis sp. and Eusyllis sp., now listed as E.spp. (1998\&2000)
- Exogone sp. and Exogone spp., now listed as E.spp. (1998\&2000)
- Harmothoe sp. and Harmothoe spp., now listed as H.spp. (1998\&2000)
- Ophiura sp and Ophiura spp. (1998\&2000)
- Typosyllis sp. and Typosyllis sp., now listed as T.spp. (1998\&2000)

Species which did not belong to the five main taxa and therefore were removed prior to data analysis:

- Acaulis primarius (Hydroida)
- Cerantius loydi (Cnidaria)
- Edwardsia sp. (Anthozoa)
- Nymphon sp. (Pycnogonida)
- Phoronis muelleri (Phoronida)
- Pboronis sp. (Phoronida)
- Priapulus caudatus (Priapulida)
- Rabdopleura normani (Hemichordata)

Table A5: Environmental variables measured in the Finnmark region IX. Variables used in the multivariate analyses are formatted bold in the header row. Abbreviations; Long: Longitude, Lat: Latitude, Md $\varphi$ : median grain size, $\mathrm{K}_{\mathrm{G}}$ : Kurtosis, Siltclay: fraction of sediment $<0.063 \mathrm{~mm}(\%), S k_{I}$ : skewness, $\sigma_{I}$ : sorting, TOM: total organic matter (\%), Temp: Temperature, Sal: Salinity

| St. | Depth | Long. | Lat. | Temp. | Salinity | Gravel | Siltclay | Sand | Md $\varphi$ | $\mathrm{K}_{\mathrm{G}}$ | $\mathrm{Sk}_{\text {I }}$ | $\sigma_{\text {I }}$ | TOM |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 160 | 19.33 | 70.75 | 6.22 | 35.03 | 30.84 | 5.85 | 63.32 | 0.67 | 0.81 | 0.09 | 2.00 | 2.13 |
| 2 | 283 | 18.67 | 70.75 | 5.97 | 34.93 | 7.30 | 33.00 | 59.70 | 2.86 | 0.93 | 0.05 | 2.83 | 3.63 |
| 3 | 238 | 18.00 | 71.00 | 5.70 | 34.98 | 0.00 | 69.78 | 30.22 | 5.13 | 0.85 | -0.09 | 1.92 | 9.37 |
| 4 | 193 | 19.00 | 71.00 | 5.82 | 35.04 | 4.03 | 31.26 | 64.71 | 3.32 | 1.27 | 0.11 | 2.31 | 3.43 |
| 5 | 190 | 20.00 | 71.00 | 6.05 | 35.01 | 0.60 | 31.78 | 67.62 | 3.40 | 1.18 | 0.21 | 2.06 | 2.80 |
| 6 | 166 | 21.00 | 71.00 | 5.36 | 34.98 | 19.55 | 12.48 | 67.97 | 1.32 | 1.03 | 0.08 | 2.38 | 1.67 |
| 7 | 228 | 21.00 | 71.25 | 5.06 | 35.04 | 0.00 | 7.30 | 92.70 | 2.68 | 1.75 | 0.20 | 0.91 | 1.27 |
| 8 | 202 | 20.00 | 71.25 | 5.74 | 35.04 | 5.15 | 12.57 | 82.28 | 1.77 | 1.45 | 0.14 | 1.96 | 2.50 |
| 9 | 235 | 20.00 | 71.50 | 5.30 | 35.07 | 2.75 | 14.80 | 82.45 | 2.83 | 1.86 | -0.02 | 1.70 | 2.93 |
| 10 | 270 | 20.00 | 71.75 | 4.71 | 35.06 | 0.55 | 72.95 | 26.50 | 5.26 | 0.97 | -0.17 | 2.01 | 10.20 |
| 11 | 316 | 21.00 | 71.75 | 3.51 | 35.03 | 0.45 | 86.90 | 12.65 | 5.70 | 1.03 | -0.14 | 1.66 | 11.33 |
| 12 | 325 | 20.87 | 71.59 | 4.50 | 35.05 | 0.24 | 61.01 | 38.75 | 4.72 | 0.75 | 0.02 | 1.98 | 9.63 |
| 13 | 325 | 20.86 | 71.59 | 4.50 | 35.05 | 0.00 | 61.30 | 38.70 | 4.74 | 0.75 | 0.04 | 1.92 | 9.20 |
| 14 | 325 | 20.84 | 71.59 | 4.50 | 35.05 | 0.35 | 50.46 | 49.19 | 4.04 | 0.83 | 0.21 | 2.00 | 5.27 |
| 15 | 325 | 20.86 | 71.59 | 4.50 | 35.05 | 0.26 | 73.43 | 26.31 | 5.28 | 0.84 | -0.08 | 1.82 | 8.70 |
| 16 | 331 | 21.08 | 71.60 | 4.17 | 35.04 | 0.21 | 67.48 | 32.31 | 5.04 | 0.93 | -0.21 | 2.30 | 6.03 |
| 17 | 321 | 21.06 | 71.60 | 4.17 | 35.04 | 0.00 | 58.87 | 41.13 | 4.60 | 0.77 | 0.12 | 1.85 | 6.37 |
| 18 | 323 | 21.05 | 71.60 | 4.17 | 35.04 | 0.25 | 84.17 | 15.58 | 5.62 | 1.02 | -0.14 | 1.71 | 9.00 |
| 19 | 321 | 21.06 | 71.61 | 4.17 | 35.04 | 0.00 | 89.84 | 10.16 | 5.77 | 1.01 | -0.13 | 1.58 | 8.80 |
| 20 | 263 | 20.42 | 71.37 | 5.32 | 35.05 | 0.00 | 65.80 | 34.20 | 4.96 | 0.79 | -0.07 | 2.00 | 8.57 |
| 21 | 260 | 20.41 | 71.36 | 5.32 | 35.05 | 4.55 | 35.31 | 60.14 | 3.07 | 1.02 | 0.14 | 2.52 | 4.03 |
| 22 | 255 | 20.40 | 71.37 | 5.32 | 35.05 | 3.18 | 19.02 | 77.80 | 2.67 | 1.78 | 0.17 | 1.95 | 2.97 |
| 23 | 263 | 20.41 | 71.37 | 5.32 | 35.05 | 0.78 | 38.11 | 61.12 | 3.43 | 0.94 | 0.28 | 2.08 | 4.83 |
| 24 | 325 | 21.00 | 71.50 | 4.32 | 35.04 | 0.76 | 79.05 | 20.19 | 5.47 | 1.08 | -0.23 | 2.01 | 7.97 |
| 25 | 361 | 22.00 | 71.75 | 3.25 | 35.02 | 0.44 | 86.28 | 13.27 | 5.68 | 1.03 | -0.14 | 1.67 | 6.33 |
| 26 | 349 | 22.00 | 71.50 | 3.39 | 35.03 | 0.00 | 92.38 | 7.62 | 5.83 | 0.96 | -0.12 | 1.50 | 8.87 |
| 27 | 365 | 23.49 | 71.50 | 3.98 | 35.03 | 0.18 | 65.77 | 34.05 | 4.96 | 0.91 | -0.01 | 1.88 | 4.40 |
| 28 | 344 | 23.46 | 71.29 | 4.11 | 35.03 | 10.46 | 8.50 | 81.03 | 2.09 | 1.45 | -0.23 | 1.89 | 2.20 |
| 29 | 278 | 22.00 | 71.25 | 4.56 | 35.05 | 2.52 | 53.32 | 44.16 | 4.25 | 0.96 | 0.04 | 2.21 | 2.30 |
| 30 | 286 | 22.00 | 71.00 | 4.86 | 35.01 | 3.93 | 30.89 | 65.17 | 3.30 | 1.45 | 0.20 | 2.15 | 3.07 |
| 31 | 270 | 20.00 | 71.75 | 4.59 | 35.06 | 0.24 | 82.62 | 17.14 | 5.58 | 1.01 | -0.15 | 1.76 | 9.21 |
| 32 | 365 | 23.49 | 70.50 | 4.32 | 35.03 | 0.00 | 69.76 | 30.24 | 5.13 | 0.80 | 0.03 | 1.70 | 4.29 |
| 33 | 255 | 27.67 | 72.25 | 4.05 | 35.04 | 0.39 | 44.74 | 54.87 | 3.81 | 0.88 | 0.32 | 1.90 | 2.33 |
| 34 | 286 | 28.00 | 72.25 | 3.92 | 35.04 | 0.67 | 61.70 | 37.64 | 4.76 | 0.85 | 0.06 | 1.86 | 3.59 |
| 35 | 288 | 28.33 | 72.25 | 3.80 | 35.04 | 0.00 | 72.61 | 27.39 | 5.25 | 0.80 | -0.04 | 1.75 | 3.89 |
| 36 | 278 | 27.67 | 72.00 | 4.07 | 35.04 | 0.32 | 57.07 | 42.60 | 4.50 | 0.86 | 0.02 | 2.11 | 4.05 |
| 37 | 280 | 28.00 | 72.00 | 4.02 | 35.04 | 1.91 | 41.78 | 56.30 | 3.69 | 0.91 | 0.39 | 1.83 | 2.61 |
| 38 | 260 | 28.33 | 72.00 | 3.90 | 35.04 | 1.91 | 48.06 | 50.03 | 3.87 | 0.97 | 0.11 | 2.28 | 2.83 |
| 39 | 294 | 29.00 | 72.00 | 3.78 | 35.04 | 0.17 | 70.09 | 29.74 | 5.15 | 0.87 | -0.04 | 1.83 | 4.33 |
| 40 | 330 | 29.67 | 71.75 | 3.46 | 35.03 | 0.00 | 65.94 | 34.06 | 4.97 | 0.84 | -0.05 | 1.96 | 4.30 |
| 41 | 340 | 30.67 | 71.62 | 3.21 | 35.01 | 0.00 | 89.75 | 10.25 | 5.77 | 0.86 | -0.07 | 1.47 | 4.51 |
| 42 | 317 | 30.67 | 71.62 | 3.21 | 35.01 | 0.00 | 76.66 | 23.34 | 5.39 | 0.77 | -0.01 | 1.61 | 3.92 |
| 43 | 294 | 30.67 | 71.50 | 3.59 | 35.01 | 0.00 | 49.74 | 50.26 | 3.99 | 0.79 | 0.37 | 1.78 | 2.77 |
| 44 | 327 | 31.17 | 71.75 | 3.10 | 35.00 | 0.00 | 91.35 | 8.65 | 5.81 | 0.88 | -0.08 | 1.46 | 5.07 |
| 45 | 321 | 31.17 | 71.62 | 3.44 | 35.00 | 0.00 | 85.82 | 14.18 | 5.67 | 0.89 | -0.09 | 1.56 | 4.56 |
| 46 | 290 | 31.17 | 71.50 | 3.82 | 35.00 | 0.00 | 79.55 | 20.45 | 5.49 | 0.81 | -0.05 | 1.62 | 3.67 |
| 47 | 315 | 17.00 | 71.50 | 5.55 | 35.12 | 4.74 | 38.77 | 56.50 | 3.38 | 1.05 | 0.11 | 2.46 | 3.94 |
| 48 | 292 | 17.33 | 71.50 | 5.44 | 35.09 | 5.28 | 26.56 | 68.16 | 2.65 | 1.10 | 0.11 | 2.58 | 3.25 |
| 49 | 279 | 17.67 | 71.50 | 5.34 | 35.09 | 3.07 | 33.39 | 63.55 | 3.41 | 1.27 | 0.15 | 2.22 | 2.94 |
| 50 | 299 | 17.00 | 71.75 | 5.41 | 35.09 | 10.30 | 30.02 | 59.68 | 2.96 | 0.95 | -0.02 | 2.83 | 3.66 |
| 51 | 311 | 17.33 | 71.75 | 5.32 | 35.09 | 0.50 | 42.52 | 56.98 | 3.71 | 0.90 | 0.22 | 2.09 | 4.32 |
| 52 | 294 | 17.67 | 71.75 | 5.23 | 35.08 | 2.11 | 36.56 | 61.32 | 3.43 | 1.04 | 0.11 | 2.37 | 4.42 |
| 53 | 331 | 17.00 | 72.00 | 5.33 | 35.10 | 2.08 | 29.89 | 68.02 | 3.16 | 1.25 | 0.25 | 2.09 | 3.25 |
| 54 | 310 | 17.33 | 72.00 | 5.22 | 35.09 | 0.61 | 40.00 | 59.39 | 3.53 | 1.00 | 0.23 | 2.15 | 4.17 |
| 55 | 300 | 17.67 | 72.00 | 5.09 | 35.08 | 0.00 | 76.26 | 23.74 | 5.38 | 0.94 | -0.15 | 1.89 | 6.96 |

a)

b)


Figure A1 a) The interpolated modeling of the temperature in the sampled area for the year 1998 b) The interpolated modeling of the temperature in the sampled area for the year 2000 . The temperature is lower in the Eastern and North-western areas both years. This figure is based on an interpolation, and the data between the data points are generated. Abbreviations: NW = North-western area, SW= South-western area and NE = North-eastern area.


Figure A2
a) The interpolated modeling of the salinity in the sampled area for the year 1998 b) The interpolated modeling of the salinity in the sampled area for the year 2000. The approximate salinity is almost uniform throughout the region. This figure is based on an interpolation, and the data between the data points are generated. Abbreviations: NW $=$ North-western area, $\mathrm{SW}=$ South-western area and NE $=$ North-eastern area.

### 6.2 Detectability and estimation of species richness

### 6.2.1 Detectability

Table A6.1: South-western area, no time effect.

| Model | Estimate | MIN(-LL) | AIC | 95\% CL | Status |
| :--- | :--- | ---: | :--- | ---: | :--- |
| $\mathrm{M}^{*} 0$ | $455.00(0.04)$ | 9140.45 | 18282.90 | $455.00-455.26$ | Converged |
| $\mathrm{M}^{*} \mathrm{~b}$ | $475.27(6.39)$ | 8483.78 | 16971.57 | $466.08-492.05$ | Converged |
| $\mathrm{M}^{*} \mathrm{~h}$ | $455.81(0.91)$ | 7330.26 | 14668.52 | $455.14-459.76$ | Converged |
| $\mathrm{M}^{*} \mathrm{bh}$ | $792.79(96.78)$ | 6827.42 | 13664.84 | $649.78-1040.77$ | Converged |

Table A6.2: South-western area, time effect.

| Model | Estimate | MIN(-LL) | AIC | $\mathbf{9 5 \%} \mathbf{C L}$ | Status |
| :--- | :---: | ---: | :--- | ---: | :---: |
| $\mathrm{M}^{*} 0$ | $455.00(0.04)$ | 9140.45 | 18282.90 | $455.00-455.26$ | Converged |
| $\mathrm{M}^{*} \mathrm{t}$ | $455.00(0.03)$ | 8430.61 | 16925.22 | $455.00-455.13$ | Converged |
| $\mathrm{M}^{*} \mathrm{~b}$ | $475.27(6.39)$ | 8483.78 | 16971.57 | $466.08-492.05$ | Converged |
| $\mathrm{M}^{*} \mathrm{~h}$ | $455.81(0.91)$ | 7330.26 | 14668.52 | $455.14-459.76$ | Converged |
| $\mathrm{M}^{*} \mathrm{tb}$ |  |  |  |  | Diverged |
| $\mathrm{M}^{*} \mathrm{th}$ | $455.40(0.64)$ | 6391.45 | 12852.90 | $455.04-458.62$ | Converged |
| $\mathrm{M}^{*} \mathrm{bh}$ | $792.79(96.78)$ | 6827.42 | 13664.84 | $649.78-1040.77$ | Converged |
| $\mathrm{M}^{*} \mathrm{tbh}$ |  |  |  |  | Diverged |

Table A6.3: North-eastern area, no time effect.

| Model | Estimate | MIN(-LL) | AIC | $\mathbf{9 5 \%} \mathbf{C L}$ | Status |
| :--- | :---: | ---: | :---: | :---: | :---: |
| $\mathrm{M}^{*} 0$ | $225.35(0.59)$ | 2077.22 | 4156.44 | $225.03-228.43$ | Converged |
| $\mathrm{M}^{*} \mathrm{~b}$ | $228.45(2.22)$ | 2051.54 | 4107.07 | $226.09-235.93$ | Converged |
| $\mathrm{M}^{*} \mathrm{~h}$ | $322.63(22.13)$ | 1351.37 | 2710.73 | $287.95-376.41$ | Converged |
| $\mathrm{M}^{*} \mathrm{bh}$ | $312.00(24.02)$ | 1351.17 | 2712.35 | $276.15-372.98$ | Converged |

Table A2.4: North-eastern area, time effect.

| Model | Estimate | MIN(-LL) | AIC | $\mathbf{9 5 \%} \mathbf{C L}$ | Status |
| :--- | :---: | ---: | :--- | :---: | :---: |
| $\mathrm{M}^{*} 0$ | $225.35(0.59)$ | 2077.22 | 4156.44 | $225.03-228.43$ | Converged |
| $\mathrm{M}^{*} \mathrm{t}$ | $225.33(0.58)$ | 2057.46 | 4142.91 | $225.03-228.36$ | Converged |
| $\mathrm{M}^{*} \mathrm{~b}$ | $228.45(2.22)$ | 2051.54 | 4107.07 | $226.09-235.93$ | Converged |
| $\mathrm{M}^{*} \mathrm{~h}$ | $322.63(22.13)$ | 1351.37 | 2710.73 | $287.95-376.41$ | Converged |
| $\mathrm{M}^{*} \mathrm{tb}$ | $276.49(28.32)$ | 1988.45 | 4006.90 | $243.80-366.02$ | Converged |
| $\mathrm{M}^{*}$ th | $323.56(22.27)$ | 1318.59 | 2671.19 | $288.64-377.64$ | Converged |
| $\mathrm{M}^{*} \mathrm{bh}$ | $312.00(24.02)$ | 1351.17 | 2712.35 | $276.15-372.98$ | Converged |
| $\mathrm{M}^{*} \mathrm{tbh}$ | $388.28(60.48)$ | 1316.95 | 2669.90 | $305.86-554.72$ | Converged |

Table A2.5: North-western area, no time effect.

| Model | Estimate | MIN(-LL) | AIC | $\mathbf{9 5 \%} \mathbf{C L}$ | Status |
| :--- | ---: | ---: | :--- | ---: | :--- |
| $\mathrm{M}^{*} 0$ | $237.82(0.92)$ | 1473.65 | 2949.31 | $237.14-241.79$ | Converged |
| $\mathrm{M}^{*} \mathrm{~b}$ | $242.29(2.83)$ | 1452.75 | 2909.50 | $238.98-251.12$ | Converged |
| $\mathrm{M}^{*} \mathrm{~h}$ | $341.17(25.01)$ | 943.47 | 1894.95 | $302.50-402.67$ | Converged |
| $\mathrm{M}^{*} \mathrm{bh}$ | $337.96(23.73)$ | 943.46 | 1896.92 | $301.09-396.05$ | Converged |

Table A2.6: North-western area, time effect.

| Model | Estimate | MIN(-LL) | AIC | 95\% CL | Status |
| :--- | ---: | ---: | ---: | ---: | :---: |
| $\mathrm{M}^{*} 0$ | $237.82(0.92)$ | 1473.65 | 2949.31 | $237.14-241.79$ | Converged |
| $\mathrm{M}^{*} \mathrm{t}$ | $237.76(0.88)$ | 1451.66 | 2921.31 | $237.12-241.65$ | Converged |
| $\mathrm{M}^{*} \mathrm{~b}$ | $242.29(2.83)$ | 1452.75 | 2909.50 | $238.98-251.12$ | Converged |
| $\mathrm{M}^{*} \mathrm{~h}$ | $341.17(25.01)$ | 943.47 | 1894.95 | $302.50-402.67$ | Converged |
| $\mathrm{M}^{*} \mathrm{tb}$ | $370.17(113.86)$ | 1394.21 | 2808.43 | $268.18-805.79$ | Converged |
| $\mathrm{M}^{*} \mathrm{th}$ | $343.93(25.80)$ | 905.87 | 1835.74 | $304.08-407.46$ | Converged |
| $\mathrm{M}^{*} \mathrm{bh}$ | $337.96(23.73)$ | 943.46 | 1896.92 | $301.09-396.05$ | Converged |
| $\mathrm{M}^{*} \mathrm{tbh}$ | $368.87(49.37)$ | 905.64 | 1837.29 | $301.84-505.18$ | Converged |

### 6.2.2 The correlation between benthic variability and environmental variation



Figure A3.1 Boxplots of the multivariate dispersion to group centroid for the three areas. Based on Euclidean distances for normalized environmental variables?

Table A3.1: Average distance to centroid.

|  | Area 1 | Area 2 | Area3 |
| :--- | :--- | :--- | :--- |
| Bray-Curtis | 0.3634 | 0.2637 | 0.2298 |
| Jaccard | 0.4748 | 0.3789 | 0.3406 |
| Chao's biascorrected | 0.2482 | 0.0688 | 0.0880 |
| Chao -abu Jaccard | 0.2135 | 0.2975 | 0.3190 |
| Euclidean-env-norm | 0.0284 | 0.0092 | 0.0062 |

### 6.3 Multivariate analyses - exploratory data analysis



Figure A3.1 A pairwise scatter plot of the five main benthic groups (abundance) in the Snow White region.
Table A3.1 Pairwise Spearman rank correlations. (Mention rel sample size\&significance?) (R) between environmental variables and applied univariate biodiversity measures ( $\mathrm{n}=55$ for all correlations). Abbreviations; Long: Longitude, Lat: Latitude, Md $\varphi$ : median grain size, $\mathrm{K}_{\mathrm{G}}$ : Kurtosis, Silt-clay: fraction of sediment $<0.063 \mathrm{~mm}(\%), S k_{I}$ : skewness, $\sigma_{\mathrm{I}}$ : sorting, TOM: total organic matter (\%), Temp: Temperature, Sal: Salinity, Exp $H^{\prime}$ : the exponential of form of the Shannon formula; 1 /Simpson's index.

|  | Dep | Long | Lat | Grav | $M d \varphi$ | $K_{G}$ | Silt | Sand | $S k_{I}$ | $\sigma_{I}$ | TOM | Temp | Sal | SpNr | $E x p H^{\prime}$ | $1 / D$ | Poly | Crus | Echi | Moll |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Long | 0.29 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Lat | 0.28 | 0.21 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Grav | -0.41 | -0.52 | -0.27 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| $M d \varphi$ | 0.54 | 0.50 | 0.40 | -0.76 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| $K_{G}$ | -0.28 | -0.43 | -0.23 | 0.61 | -0.43 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Silt | 0.54 | 0.49 | 0.39 | -0.74 | 0.99 | -0.45 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Sand | -0.54 | -0.49 | -0.38 | 0.70 | -0.98 | 0.49 | -0.99 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| $S k_{I}$ | -0.40 | -0.22 | -0.10 | 0.34 | -0.66 | 0.09 | -0.66 | 0.69 |  |  |  |  |  |  |  |  |  |  |  |  |
| $\sigma_{I}$ | -0.33 | -0.60 | -0.17 | 0.70 | -0.63 | 0.27 | -0.60 | 0.58 | 0.37 |  |  |  |  |  |  |  |  |  |  |  |
| TOM | 0.49 | -0.03 | 0.23 | -0.53 | 0.74 | -0.33 | 0.75 | -0.73 | -0.59 | -0.26 |  |  |  |  |  |  |  |  |  |  |
| Temp | -0.57 | -0.87 | -0.51 | 0.62 | -0.72 | 0.41 | -0.70 | 0.69 | 0.38 | 0.68 | -0.27 |  |  |  |  |  |  |  |  |  |
| Sal | -0.05 | -0.64 | 0.30 | 0.29 | -0.25 | 0.23 | -0.24 | 0.27 | 0.20 | 0.42 | 0.12 | 0.41 |  |  |  |  |  |  |  |  |
| SpNr | -0.48 | -0.60 | -0.29 | 0.49 | -0.58 | 0.35 | -0.58 | 0.57 | 0.45 | 0.55 | -0.22 | 0.67 | 0.18 |  |  |  |  |  |  |  |
| ExpH' | -0.42 | -0.69 | -0.45 | 0.62 | -0.63 | 0.41 | -0.62 | 0.61 | 0.37 | 0.65 | -0.17 | 0.75 | 0.25 | 0.84 |  |  |  |  |  |  |
| $1 / D$ | -0.31 | -0.57 | -0.49 | 0.58 | -0.59 | 0.32 | -0.57 | 0.56 | 0.25 | 0.56 | -0.14 | 0.64 | 0.20 | 0.63 | 0.92 |  |  |  |  |  |
| Poly | -0.27 | 0.02 | 0.22 | 0.05 | -0.19 | 0.00 | -0.22 | 0.22 | 0.39 | 0.12 | -0.28 | 0.05 | -0.11 | 0.51 | 0.07 | -0.12 |  |  |  |  |
| Crus | -0.20 | -0.35 | 0.06 | 0.32 | -0.29 | 0.21 | -0.29 | 0.30 | 0.24 | 0.42 | -0.01 | 0.30 | 0.27 | 0.72 | 0.61 | 0.49 | 0.40 |  |  |  |
| Echi | -0.16 | -0.66 | -0.21 | 0.37 | -0.29 | 0.29 | -0.27 | 0.28 | 0.20 | 0.47 | 0.15 | 0.55 | 0.43 | 0.62 | 0.69 | 0.62 | 0.01 | 0.45 |  |  |
| Moll | -0.28 | 0.01 | 0.36 | 0.07 | -0.19 | -0.08 | -0.19 | 0.19 | 0.41 | 0.20 | -0.35 | 0.04 | 0.03 | 0.31 | -0.01 | -0.13 | 0.66 | 0.26 | 0.01 |  |
| Sipu | 0.14 | -0.10 | 0.35 | -0.16 | 0.30 | -0.01 | 0.29 | -0.27 | -0.06 | -0.07 | 0.26 | -0.08 | 0.06 | 0.09 | -0.13 | -0.25 | 0.35 | 0.13 | 0.11 | 0.25 |



Figure A3.2 A pairwise scatter plot of environmental variables in the Snow White region. Abbrevations: Abbreviations; Sal: Salinity, Temp: Temperature, TOM: total organic matter (\%), Sort: Sorting ( $\sigma_{\mathrm{I}}$ ), Skewness: Skewn (Sk), Sand, Siltc: Silt-clay fraction of sediment $<0.063 \mathrm{~mm}(\%)$, Kurt: Kurtosis, Grains: Grainsize (md $\varphi$ ), Gravel, Lat: Latitude, Long: Longitude. Salinity and temperature are approximate values (view methods 2.2, figure A1and A2).


Figure A3.3 A Canonical Correspondence analysis (CCA). The triplot shows the samples (1 to 55 ), the response variables (taxonomical groups in red) and the quantitative predictor variables (Temperature, TOM, Sorting, Skewness, Grainsize, Latitude, Longitude and Depth). The percentage of variation explained in figure 11 is $38.69 \%$. CCA-2-axis explains $7.23 \%$ and the CCA3-axis $5.30 \%$. (CCA4-axis explains $1.67 \%$ ).


Figure A3.4 A Canonical Correspondence analysis (CCA) plot. The percentage of variation explained in figure 11 is $48.87 \%$. CCA-2-axis explained $7.55 \%$ and the CCA3-axis $7.55 \%$. The CCA4-axis explained $3.02 \%$.


Figure A3.5 A Canonical Correspondence analysis (CCA) plot. The percentage of variation explained (all axes) is $43.25 \%$. CCA2-axis explained $9.83 \%$, CCA3-axis explained $6.15 \%$. The unplotted CCA4-axis explained 2.03\%.
Feeding guild and functional groups database.
detr. Ss.detr. Omni. Inf/Epi Abu. (log)

$\qquad$
$\qquad$

$$
000000000000000000000000000000000000000000000000000000
$$

$$
-1-1000000000000-1-10000000000001-1-10000000000000000-
$$

$$
00000000000000000000000 \sim-\cdots+-T-1000000000000000000-00
$$

$$
000 \cdots \cdots \cdots \cdots \cdots-\cdots-\cdots-\cdots-\cdots-\cdots 0000000000000000000000000000
$$




| Species | Family (overfam.) | Source | Mobile | Discr. mob. | Non-mob. | Mobility | Susp. | Carn | S.detr. | Ss.detr. | Omni. | Inf/Epi | Abu. (log) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Maera sp. | Melitidae | Biernbaum 1979, Crawford 1937, Enequist 1949 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Aceroides latipes | Oedicerotidae | Enequist 1949 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Paroediceros sp. | Oedicerotidae | Enequist 1949 | 1 | 0 | 0 | , | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Syncbelidium tenuimanum | Oedicerotidae | Chevrier et al. 1991 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.69 |
| Arrbis phyllonyx | Oedicerotidae | Enequist 1949 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Monoculodes packardi | Oedicerotidae | Chevrier et al. 1991 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Monoculodes sp. | Oedicerotidae | Chevrier et al. 1991 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.69 |
| Battymedon longimanus | Oedicierotidae | Chevrier et al. 1991 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Bathymedon saussurei | Oedicierotidae | Chevrier et al. 1991 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2.10 |
| Bathymedon sp. | Oedicierotidae | Chevrier et al. 1991 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Halice abyssi | Pardaliscidae | Miskov-Nodland et al. 1999 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 3.30 |
| Nicippe tumida | Pardaliscidae | Miskov-Nodland et al. 1999 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2.61 |
| Pardalisca alyssi | Pardaliscidae | Enequist 1949 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2.95 |
| Harpinia antennaria | Phoxocephalidae | Enckell 1998, Buhl-Mortensen 1996, Miskov-Nodland et al. 1999 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 6.19 |
| Harpinia crenulata | Phoxocephalidae | Enckell 1998, Buhl-Mortensen 1996, Miskov-Nodland et al. 1999 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 5.04 |
| Harpinia laevis | Phoxocephalidae | Enckell 1998, Buhl-Mortensen 1996, Miskov-Nodland et al. 1999 | 0 | 1 | 0 | , | 0 | 0 | 1 | 0 | 0 | 0 | 1.00 |
| Harpinia mucronata | Phoxocephalidae | Enckell 1998, Buhl-Mortensen 1996, Miskov-Nodland et al. 1999 | 0 | 1 | 0 | , | 0 | 0 | 1 | 0 | 0 | 0 | 5.25 |
| Harpinia pectinata | Phoxocephalidae | Enckell 1998, Buhl-Mortensen 1996, Miskov-Nodland et al. 1999 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 5.89 |
| Harpinia sp. | Phoxocephalidae | Enckell 1998, Buhl-Mortensen 1996, Miskov-Nodland et al. 1999 | 0 | 1 | 0 | , | 0 | 0 | 1 | 0 | 0 | 0 | 2.10 |
| Leptophoxus falcatus | Phoxocephalidae | Enckell 1998, Buhl-Mortensen 1996, Miskov-Nodland et al. 1999 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 3.71 |
| Paraphoxus oculatus | Phoxocephalidae | Enckell 1998, Buhl-Mortensen 1996, Miskov-Nodland et al. 1999 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 3.56 |
| Pboxocephalus holbolli | Phoxocephalidae | Enckell 1998, Buhl-Mortensen 1996, Miskov-Nodland et al. 1999 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |  | 0 | 2.79 |
| Dulichia sp. | Podoceridae | Chevrier et al. 1991, Enequist 1949, Dziaduch 2007 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2.61 |
| Laetmatophilus tuberculatus | Podoceridae | Buhl-Mortensen 1996, Enequist 1949 | 0 | 1 | 0 | , | 1 | 0 | 0 | 0 | 0 | 1 | 3.30 |
| Xenodice frauenfeldit | Podoceridae | Biernbaum 1979, Enequist 1949 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2.79 |
| Ischyrocerus sp. | Ischyroceridae | Kuris et al. 1991, Enequist 1949, Buhl-Mortensen \& Mortensen 2005 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 4.00 |
| Andaniella pectinata | Stegocephalidae | De Broyer et al. 2004 | 1 | 0 | 0 | , | 0 | 1 | 0 | 0 | 0 | 1 | 1.69 |
| Metopa boecki | Stenothoidae | Chevrier et al. 1991 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1.00 |
| Metopa glacialis | Stenothoidae | Chevrier et al. 1991, Biernbaum 1979, Thiel 1999 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1.69 |
| Stenotboe brevicornis | Stenothoidae | Chevrier et al. 1991, Biernbaum 1979, Vader \& Krapp-Schickel 1996 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1.69 |
| Stenotboe marina | Stenothoidae | Chevrier et al. 1991, Biernbaum 1979, Krapp-Schickel 1993 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1.69 |
| Stenotboe monoculoides | Stenothoidae | Koukouras et al. 1996, Vader \& Krapp-Schickel 1996 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1.00 |
| Bruzelia tuberculata | Synopiidae | Enequist 1949 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Syrrboites serratus | Synopiidae | Enckell 1998 | 0 | 1 | 0 | , | 0 | 0 | 1 | 0 | 0 | 1 | 2.39 |
| Tiron sp. | Synopiidae | Enequist 1949 | 0 | 1 | 0 | , | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Urotboe elegans | Urothoidae | Enequist 1949 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 5.36 |
| Campylaspis costata | Nannastacidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | , | 0 | 0 | 2.39 |
| Campylastis glabra | Nannastacidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | , | 0 | 0 | 0 | 1 | 0 | 0 | 3.30 |
| Campylaspis horrida | Nannastacidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | , | 0 | 0 | 0 | 1 |  | 0 | 2.95 |
| Campylaspis sulcata | Nannastacidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1.00 |
| Campylaspis undata | Nannastacidae | Stransky 2007, Enckell 1998 |  | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 5.01 |
| Campylaspis verrucosa | Nannastacidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2.79 |
| Iphinoe trispinosa | Bodotriidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1.00 |
| Diastyloides biplicata | Diastylidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2.10 |
| Diastyloides serrata | Diastylidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1.00 |
| Diastylis cornuta | Diastylidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | , | 0 | 0 | 0 | 1 | 0 | 1 | 2.61 |
| Diastylis echinata | Diastylidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | , | 0 | 0 | 0 | 1 | 0 | 1 | 2.61 |
| Diastylis lucijera | Diastylidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1.69 |
| Diastylis spinulosa | Diastylidae | Stransky 2007, Enckell 1998 |  | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1.69 |
| Diastylis tumida | Diastylidae | Stransky 2007, Enckell 1998 |  | 1 | 0 | , | 0 | 0 | 0 | 1 | 0 | 1 | 1.69 |
| Diastylis spp. | Diastylidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | , | 0 | 0 | 0 | , | 0 | 1 | 2.95 |
| Eudorella truncatula | Leuconidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 3.30 |
| Leucon spp. | Leuconidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | , | 0 | 0 | 0 |  | 0 | 0 | 4.91 |
| Hemilamprops cristata | Lampropidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 3.56 |
| Hemilamprops roseus | Lampropidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1.69 |
| Hemilamprops uniplicata | Lampropidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | , | 0 | 0 | 2.95 |
| Playsympus typicus | Lampropidae | Stransky 2007, Enckell 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |  | 0 | 0 | 1.00 |
| Strongl/ura a ylindrata | Parathanaidae | Holdich \& Jones 1983 in Stransky 2007 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2.61 |
| Apseudes spinosus | Apseudidae | Holdich \& Jones 1983 in Stransky 2007 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 4.69 |


| Species | Family (overfam.) | Source | Mobile | Discr. mob. | Non-mob. | Mobility | Susp. | Carn | S.detr. | Ss.detr. | Omni. | Inf/Epi | Abu. (log) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Typhlotanais sp. | Nototainaidae | Holdich \& Jones 1983 in Stransky 2007 | 1 | 0 | 0 | , |  | 0 | 1 | 0 | 0 | 0 | 2.95 |
| Pseudosphyrapus anomalus | Sphyrapidae | Hop et al. 2002 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 3.77 |
| Scalpellum sp. | Scalpellidae | Gibson et al. 2001 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1.69 |
| Pontophilus norvegicus | Crangonidae | Maynou \& Cartes 1998, Cartes et al. 2007 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2.10 |
| Geyon trispinosus | Gergonidae | Cartes et al. 2007 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1.69 |
| Hyas araneus | Brachyura | Pers.obs. | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1.69 |
| Calathura brachiata | Anthuridae | Svavarsson \& Olafsdottir 1999, Wetzer et al. 1997 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 4.74 |
| Astacilla longicornis | Arcturidae | Poore 2001 in Stransky \& Svavarsson 2006 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1.69 |
| Eurydice sp. | Cirolanidae | Enckell 1998, Keable 1995 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 2.61 |
| Eurydice truncata | Cirolanidae | Enckell 1998, Keable 1995 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 5.14 |
| Natatolana borealis | Cirolanidae | Enckell 1998, Keable 1995 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.69 |
| Dendrotion spinosum | Dendrotionidae | Hessler \& Thistle 1975, Wolff 1962 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4.66 |
| Desmosomella armatum | Desmosomatidae | Hessler \& Strömberg 1989, Wilson \& Hessler 1987, Hult 1941 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2.10 |
| Ecbinopleura aculeata | Desmosomatidae | Hessler \& Strömberg 1989, Wilson \& Hessler 1987, Hult 1941 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2.95 |
| Whoia angusta | Desmosomatidae | Hessler \& Strömberg 1989, Wilson \& Hessler 1987, Hult 1941 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2.95 |
| Euryope producta | Eurycopidae | Hessler \& Strömberg 1989, Hessler \& Thistle 1975, Hult 1941 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Euryope sp. | Eurycopidae | Hessler \& Strömberg 1989, Hessler \& Thistle 1975, Hult 1941 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2.39 |
| Gnathia abyssorum | Gnathiidae | Enckell 1998, Wetzer et al. 1997, Klitgaard 1995 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 2.79 |
| Gnathia elongata | Gnathiidae | Enckell 1998, Wetzer et al. 1997 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 3.40 |
| Gnathia birsuta | Gnathiidae | Enckell 1998, Wetzer et al. 1997 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 3.20 |
| Gnatbia oxyurea | Gnathiidae | Enckell 1998, Wetzer et al. 1997 | 1 | 0 | 0 | 1 | 0 | , | 0 | 0 | 0 | 1 | 3.77 |
| Gnathia sp. | Gnathiidae | Enckell 1998, Wetzer et al. 1997 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 3.48 |
| Ischnomesus bispinosus | Ischnomesidae | Hessler \& Strömberg 1989,Hessler \& Thistle 1975,Wilson \& Hessler 1987 | 0 | 1 | 0 | 1 |  |  | 0 | 0 | 1 | 1 | 3.08 |
| Aspidarachna clypeata | Ilyarachnidae | Hessler \& Strömberg 1989, Hessler \& Thistle 1975 | 1 | 0 | 0 | 1 | 0 |  | 1 | 0 | 0 | 1 | 1.69 |
| Iolella lacinata | Janiridae | Hessler \& Strömberg 1989 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.69 |
| Janira maculosa | Janiridae | Koukouras et al. 1996, Stransky 2007 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 3.89 |
| Macrostylis longiremis | Macrostylidae | Hessler \& Strömberg 1989 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 3.71 |
| Macrostylis spinijera | Macrostylidae | Hessler \& Strömberg 1989 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1.69 |
| IJarachna longicornis | Munnopsidae | Brandt et al. 2004, Irina Malyutina pers.comm. Wolff 1962 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4.93 |
| Echinozone coronata | Munnopsidae | Brandt et al. 2004, Irina Malyutina pers.comm. Wolff 1962 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1.69 |
| Nannoniscus oblongus | Nannoniscidae | Wetzer et al. 1997, Wilson \& Hessler 1987 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 4.85 |
| Leptantbura tenuis | Paranthuridae | Wetzer et al. 1997. | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 4.37 |
| Nebalia bipes | Neballidae | Lee \& Morton 2005, Hayward \& Ryland 1990 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 4.40 |
| Nebalia typhlops | Neballidae | Lee \& Morton 2005 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| Munida sarsi | Galatheidae | Karas et al. 2007 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2.10 |
| Munida sp. | Galatheidae | Karas et al. 2007 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 2.79 |
| Munna spp. | Munnidae | Hessler \& Strömberg 1989 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 4.37 |
| Philomedes lilljeborgi | Cypridinidae | Parker 2000, Heger et al. 2007, Keable 1995 | 1 | 0 | 0 | 1 |  |  | 0 | 0 | 0 | 1 | 3.40 |
| $V$ argula norvegica | Cypridinidae | Parker 2000, Heger et al. 2007, Keable 1995 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 7.28 |
| Macrogpris minna | Macrocypridae | Maddocks 1977 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2.61 |
| Macroypris sp. | Macrocypridae | Maddocks 1977 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 5.38 |
| Echinodermata |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Amphilepis norvegica | Amphilepitididae | Mortensen 1927, Warner 1982 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1.00 |
| Amphipholis squamata | Amphilepitididae | Mortensen 1927, Klitgaard 1995, Warner 1982 | 1 | 0 | 0 | 1 | , |  | 0 | 0 | 1 | 1 | 6.70 |
| Amphiura borealis | Amphiuridae | Mortensen 1927, Warner 1982 | 1 | 0 | 0 | 1 | 0 |  | 0 | 0 | 1 | 1 | 4.43 |
| Ampbiura securigera | Amphiuridae | Mortensen 1927, Warner 1982 | 0 | 1 | 0 | 1 | 0 |  | 0 | 0 | 1 | 0 | 4.37 |
| Amphiura spp. | Amphiuridae | Mortensen 1927, Warner 1982 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2.61 |
| Pontaster tenuispinus | Benthopectinidae | Mortensen 1927 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | , | 1 | 2.10 |
| Henricia sanguinolenta | Echinasteridae | Moen \& Svendsen 2004 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| Ophiacantba abyssicola | Ophiacanthidae | Mortensen 1927, Warner 1982 | 0 | 1 | 0 | 1 |  | 0 | 0 | 0 | 1 | 1 | 5.96 |
| Ophiacantha bidentata | Ophiacanthidae | Mortensen 1927, Warner 1982 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1.00 |
| Ophiactis abyssicola | Ophiactidae | Mortensen 1927, Warner 1982 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1.00 |
| Ophiactis balli | Ophiactidae | Mortensen 1927, Warner 1982 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1.00 |
| Ophiopholis aculeata | Ophiactidae | Mortensen 1927, Warner 1982 | 1 | 0 | 0 | 1 | O | 0 | 0 | 0 | 1 | 1 | 4.53 |
| Ophiosolex glacialis | Ophioscolex | Rowe et al. 1997, Warner 1982 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2.95 |
| Ophiothrix fragilis | Ophiothrix | Mortensen 1927, Warner 1982 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 3.08 |
| Ophiura affinis | Ophiura | Mortensen 1927, Tyler et al. 2005, Warner 1982 | 1 | 0 | 0 | 1 | , | 0 | 0 | 0 | 1 | 1 | 2.10 |
| Ophiura albida | Ophiura | Mortensen 1927, Tyler et al. 2005, Warner 1982 | 1 | 0 | 0 | 1 |  | 0 | 0 | 0 | 1 | 1 | 3.08 |
| Ophiura sarsii | Ophiura | Mortensen 1927, Tyler et al. 2005, Warner 1982 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 4.30 |



Skeneidae
Skeneidae
Skeneidae
Skeneidae
Trichotropid
Trichotropid
Trochidae
Trochidae
Vasidae
Velutinidae


$$
\begin{aligned}
& \text { Aitken \& Gilbert } 1996 \\
& \text { Aitken \& Gilbert } 1996 \\
& \text { H }
\end{aligned}
$$

Hayward \& Ryland 1990,
Hayward \& Ryland 1990, Valentine et al. 2002, Todd 2001
Hayward \& Ryland 1990, Valentine et al. 2002, Todd 2001
Hayward \& Ryland 1990, Valentine et al. 2002, Todd 2001
Aitken \& Gilbert 1996 , Hayward \& Ryland 1990, Todd 2001, Klitgaard 1995
Hayward \& Ryland 1990, Todd 2001, Klitgaard 1995
Hayward \& Ryland 1990, Todd 2001
Taylor unpublished in Valentine et al. 2002 Taylor unpublished in Valentine et al. 2002
Hayward \& Ryland 1990 Kirkegaard 1992
Kirkegaard 1992 Kirkegaard 1992 Fauchald \& Jumars 1979, Kirkegaard 1992 Fauchald \& Jumars 1979, Kirkegaard 1992
Fauchald \& Jumars 1979, Kirkegaard 1992 Fauchald \& Jumars 1979, Kirkegaard 1992
Fauchald \& Jumars 1979, Kirkegaard 1992 Fauchald \& Jumars 1979, Kirkegaard 1992
Fauchald \& Jumars 1979, Kirkegard 1992
 Fauchald \& Jumars 1979, Kirkegaard 1992
Fauchald \& Jumars 1979, Kirkegaard 1992 Fauchald \& Jumars 1979, Kirkegaard 1992
Fauchald \& Jumars 1979, Kirkegaard 1992

 Fauchald \& Jumars 1979, Kirkegaard 1992
Fauchald \& Jumars 1979, Kirkegaard 1992
 Fauchald \& Jumars 1979, Kirkegaard 1992
Fauchald \& Jumars 1979, Kirkegaard 1992 Fauchald \& Jumars 1979, Kirkegaard 1992
Fauchald \& Jumars 1979, Kirkegaard 1992 Fauchald \& Jumars 197, Kirkegaard 1902
 Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998



| Species | Family (overfam.) | Source | Mobile | Discr. mob. | Non-mob. | Mobility | Susp. | Carn | S.detr. | Ss.detr. | Omni. | Inf/Epi | Abu. (log) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Skenea basistriata | Skeneidae | Hayward \& Ryland 1990, Valentine et al. 2002, Todd 2001 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |  | 2.10 |
| Skenea peterseni | Skeneidae | Hayward \& Ryland 1990, Valentine et al. 2002, Todd 2001 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.69 |
| Skenea sp. | Skeneidae | Hayward \& Ryland 1990, Valentine et al. 2002, Todd 2001 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Skenea trochoides | Skeneidae | Hayward \& Ryland 1990, Valentine et al. 2002, Todd 2001 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2.10 |
| Trichotropis boralis | Trichotropidae | Aitken \& Gilbert 1996 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1.00 |
| Trichotropis sp. | Trichotropidae | Aitken \& Gilbert 1996 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1.00 |
| Margarites costalis | Trochidae | Hayward \& Ryland 1990, Todd 2001, Klitgaard 1995 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Solariella obscura | Trochidae | Hayward \& Ryland 1990, Todd 2001 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Metzgeria alba | Vasidae | Taylor unpublished in Valentine et al. 2002 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| $V$ elutina undata | Velutinidae | Hayward \& Ryland 1990 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| Polychaeta |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Macrochaeta clavicornis | Acrociridae | Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2.10 |
| Macrochaeta polyoryx | Acrociridae | Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 4.14 |
| Macrochaeta spp. | Acrociridae | Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2.79 |
| Amage auricula | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 5.62 |
| Amagopsis klugei | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2.10 |
| Ampharete baltica | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2.39 |
| Ampharete falcata | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 4.04 |
| Ampharete finmarrbica | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3.94 |
| Ampharete lindstroemi | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 4.37 |
| Amphicteis gunneri | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 4.93 |
| Amythasides macroglossus | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 7.19 |
| Anobothrus gracilis | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2.95 |
| Echssippe vanelli | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 5.23 |
| Glyphanostomum pallessens | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3.30 |
| Lysippides fragilis | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3.77 |
| Melinna cristata | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3.77 |
| Mugga wabrbeergi | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3.64 |
| Sabellides borealis | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Sabelides octocirrata | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 4.40 |
| Samytba sexcirrata | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 4.26 |
| Samytbella neglecta | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 4.53 |
| Sosane sulcata | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3.71 |
| Sosanopsis wirni | Ampharetidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 |  | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3.64 |
| Euphrosine borealis | Euphrosinidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| Hermodice carunculata | Amphinomidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 4.61 |
| Paramphinome jeffressii | Amphinomidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 8.34 |
| Pareurytboe borealis | Amphinomidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 4.26 |
| Apistobranchus tullbergi | Apistobranchidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | O | 0 | 0 | 2.79 |
| Drilonereis filum | Arabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 2.39 |
| Drilonereis sp. | Arabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | , | 0 | 1 | 1.69 |
| Capitella capitata | Capitellidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2.95 |
| Heteromastus filiformis | Capitellidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 7.98 |
| Mediomastus sp. | Capitellidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1.00 |
| Notomastus spp. | Capitellidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 8.27 |
| Spiochaetopterus sp. | Chaetopteridae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1.00 |
| Spiochaetopterus typicus | Chaetop teridae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 5.79 |
| Phyllochaetopterus sp. | Chaetopteridae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | , | 0 | 0 | 3.64 |
| Caulleriella bioculata | Cirratulidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |  | 0 | 0 | 3.48 |
| Caulleriella serrata | Cirratulidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | , | 0 | 1 | 0 | 0 | 1 |  | 0 | 0 | 5.78 |
| Caulleriella spp. | Cirratulidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | , | 0 | 1 | 0 | 0 | 1 |  | 0 | 1 | 3.89 |
| Cbaetozone setosa complex | Cirratulidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |  | 0 | 1 | 7.70 |
| Cirratulus cirratus | Cirratulidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | , | 0 | 1 | 3.64 |
| Thayxx killariensis | Cirratulidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 5.91 |
| Thayx sp. | Cirratulidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 6.94 |
| Cossura longocirata | Cossuridae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 7.11 |
| Ophryotrocha sp. | Dorvilleidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 3.08 |
| Parougia caeca | Dorvilleidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | , | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 3.48 |
| Protodorvillea kefersteini | Dorvilleidae | Fauchald \& Jumars 1979, Kirkegaard 1992 |  | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 5.70 |



| Species | Family (overfam.) | Source | Mobile | Discr. mob. | Non-mob. | Mobility | Susp. | Carn | S.detr. | Ss.detr. | Omni. | Inf/Epi | Abu. (log) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Paradiopatra quadricuspis | Onuphidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 5.32 |
| Ophelina abranchiata | Ophelidae | Holte 1998, Fauchald \& Jumars 1979 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 7.78 |
| Opbelina acuminata | Ophelidae | Holte 1998, Fauchald \& Jumars 1979 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1.00 |
| Opbelina cylindricaudata | Ophelidae | Holte 1998, Fauchald \& Jumars 1979 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |  | 0 | 6.66 |
| Ophelina modesta | Ophelidae | Holte 1998, Fauchald \& Jumars 1979 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 5.17 |
| Scoloplos armiger | Orbiniidae | Holte 1998, Fauchald \& Jumars 1979 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 6.06 |
| Orbinia sertulata | Orbiniidae | Holte 1998, Fauchald \& Jumars 1979 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1.00 |
| Pbylo norvegica | Orbiniidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 5.09 |
| Myriochele danielsseni | Owenidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 6.31 |
| Myriochele fragilis | Owenidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 7.30 |
| Myriocbele beeri | Owenidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 5.16 |
| Myriochele oculata | Owenidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 5.06 |
| Owenia fusiformis | Oweniidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 4.09 |
| Aricidea catberinae | Paraonidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 6.14 |
| Aricidea laubieri | Paraonidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2.10 |
| Aricidea roberti | Paraonidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2.61 |
| Aricidea simonae | Paraonidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 4.18 |
| Aricidea sp. | Paraonidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 6.76 |
| Aricidea suecica | Paraonidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | , | 0 | 4.87 |
| Levinsenia gracilis | Paraonidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 5.88 |
| Paradoneis bra | Paraonidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 7.82 |
| Pectinaria auricoma | Pectinaridae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |  | 0 | 2.10 |
| Pectinaria sp. | Pectinaridae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2.39 |
| Eteone flava | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992, Holte 1998 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1.00 |
| Eteone sp. | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 3.48 |
| Eulalia bilineata | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| Eulalia hanssoni | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| Eulalia mustela | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.69 |
| Eulalia sp. | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| Notophyllum foliosum | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | , | 0 | 1 | 0 | 0 |  | 1 | 1.69 |
| Paranaitis wablleergi | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |  | 1 | 2.79 |
| Pbyllodoce groenlandica | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 3.08 |
| Phyllodoce longipes | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 4.04 |
| Sige oliveri | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 2.10 |
| Eumida babusiensis | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| Eumida ockelmanni | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| Eumida sannuinea | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.00 |
| Mystides borealis | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.69 |
| Mystides caeca | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1.69 |
| Protomystides exigua | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 4.69 |
| Psendomystides limbata | Phyllodocidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 2.10 |
| Ancistrosyllis sp. | Pilargidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 2.10 |
| Pisione remota | Pisionidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1.69 |
| Branchiomma bombyx | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 3.48 |
| Chone collaris | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2.95 |
| Chone duneri | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 5.83 |
| Cbone spp. | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 6.48 |
| Euchone analis | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 |  | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 4.50 |
| Euchone incolor | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 7.15 |
| Euchone sp. | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | , | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 5.98 |
| Jasmineira candela | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | , | 0 | 1 | 0 | 0 | 0 |  | 1 | 3.40 |
| Jasmineira caulata | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2.39 |
| Jasmineira elegans | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 5.82 |
| Perkinsiana sp. | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1.00 |
| Potamilla neglecta | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1.00 |
| Potamilla reniformis | Sabellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |  | 1 | 3.48 |
| Sclerocheilus minutus | Scalibregmidae | Holte 1998/Fauchald \& Jumars 1979 | 0 | 1 | 0 | , | 0 | 0 | 0 | 1 | 0 | 0 | 4.04 |
| Lipobranchus jeffressii | Scalibregmidae | Holte 1998/Fauchald \& Jumars 1979 | 0 |  | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 5.28 |
| Polyphysia crassa | Scalibregmidae | Holte 1998/Fauchald \& Jumars 1979 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2.10 |



| Species | Family (overfam.) | Source | Mobile | Discr. mob. | Non-mob. | Mobility | Susp. | Carn | S.detr. | Ss.detr. | Omni. | Inf/Epi | Abu. (log) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Pobcirrus medusa | Terebellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 6.60 |
| Polycirus norvegicus | Terebellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3.89 |
| Pobcirrus plumosus | Terebellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2.10 |
| Proclea grafi | Terebellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 5.36 |
| Proclea malmgreni | Terebellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2.61 |
| Streblosoma bairdi | Terebellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1.00 |
| Streblosoma intestinale | Terebellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2.10 |
| Artacama proboscidea | Terebellidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1.69 |
| Octobrancbus floricps | Trichobranchidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | , | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 6.93 |
| Terebelides stroemi | Trichobranchidae | Fauchald \& Jumars 1979, Kirkegaard 1992 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 7.16 |
| Sipuncula |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Oncbnesoma squamatum | Phascolionidae | Hayward \& Ryland 1990, Sheridan 1997 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |  | 1 | 6.70 |
| Oncbnesoma steenstrupi | Phascolionidae | Hayward \& Ryland 1990, Sheridan 1997 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |  | 0 | 6.63 |
| Golfingia elongata | Golfingiidae | Hayward \& Ryland 1990, Sheridan 1997 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 3.08 |
| Golfingia margaritacea | Golfingiidae | Hayward \& Ryland 1990, Sheridan 1997 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 6.36 |
| Golfingia minuta | Golfingiidae | Hayward \& Ryland 1990, Sheridan 1997 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 4.89 |
| Golfingia vulgaris | Golfingiidae | Hayward \& Ryland 1990, Sheridan 1997 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 7.12 |
| Golfingia spp. | Golfingiidae | Hayward \& Ryland 1990, Sheridan 1997 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 8.07 |
| Phascolion strombi | Phascolionidae | Hayward \& Ryland 1990, Sheridan 1997 | 0 | 1 | 0 | 1 | 0 | 0 | , | 0 | 0 | 0 | 4.14 |
| Sipunculus norvegicus | Sipunculidae | Hayward \& Ryland 1990, Sheridan 1997 | , | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1.69 |

