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Soft bottom benthos and responses to climate variation and eutrophication in Skagerrak

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Abstract

Skagerrak has been subject to several anthropogenic influences over the past decades, with climate change and eutrophication being considered as the most serious and large-scale disturbance factors. The present study reports monitoring data from six soft bottom stations in 50-380 m depth at the Norwegian Skagerrak coast aimed at investigating to which degree changes in environmental conditions have affected species communities and diversity. Sampling was carried out yearly in the period 1990-2010. Links between benthic community patterns and climate factors and physicochemical variables from the water mases were examined using uni- and multivariate statistical methods. Throughout the period species richness gradually increased. Although all stations showed distinct species assemblages, the community composition gradually changed towards increased importance of sensitive small molluscs and tube-building annelids concurrent with a general temperature increase and reduction of nutrients in the water masses. The trend was largely similar over the stations, indicating that large-scale changes in the Skagerrak water masses were driving factors compared to possible influences from local sources. The faunal changes during the study period thus indicate an improved status of the soft bottom benthos, which possibly could be related to a reduction in the eutrophication. On a shorter scale, species richness was found to vary in relation to North Atlantic Oscillation (NAO) Index in the previous year (decline), nutrient concentrations in spring (decline), and winter water temperature (incline).

Keywords: Soft bottom benthos, species richness, climate change, eutrophication, time-series

1. INTRODUCTION

Climate change is both a global and a regional challenge. In the North Sea, water temperature has increased 1-2 ºC since 1985 (OSPAR 2010), and benthic communities have been documented to be affected by temperature changes (e.g. Kröncke et al. 1998; Kröncke et al. 2011; Neumann & Kröncke 2011). Climatic induced shifts in diversity patterns and species ranges have been observed along the Norwegian coast (Narayanaswamy et al. 2010). Increasing temperature is expected to increase the global rate of species extinction (Thomas et al. 2004), but in the coastal zone indirect effects of climate change caused by e.g. increased runoff from land and increased stratification may be more important on a short term. Frigstad et al. (2013) documented a regime shift in seston and non-autotrophic material in coastal waters of the Norwegian Skagerrak early in the 2000s, and suggested that effects of increased freshwater runoff, especially increased inputs of terrestrial-derived, humic material, could play a role in the observed changes. At the same time remarkable biological changes took place in the coastal waters, e.g. reduction in sugar kelp

Saccharina latissima (Moy & Christie 2012) and reduction in recruitment of fish (Johannessen et al. 2011). Eutrophication has been one of the most serious and challenging environmental problems both on a global scale and in the North Sea (OSPAR 2010) and Skagerrak (Boesch et al. 2006). Due to management effort, regional inputs of nutrients by ocean currents from the south North Sea have decreased during the last two decades (Aure & Magnusson 2008, Vermaat et al. 2008). On the other hand, inputs from some rivers and aquaculture have increased (Skarbøvik et al. 2010), and there is evidence of an increase in terrestrial-derived matter in coastal waters (Frigstad et al. 2013).

Climate changes and eutrophication affect species composition of pelagic as well as benthic ecosystems. Benthic communities are particularly suited for monitoring as the constituent species are mainly sessile and integrate long-term effects of environmental change over time (Gray et al. 1990). As the species vary in sensitivity, the benthic communities undergo changes in composition corresponding to the degree of disturbances (Pearson & Rosenberg 1978, Bilyard 1987, Olsgard & Gray 1995). In this regard, it is important to be aware that the long time-interval over which degradation has occurred makes it difficult to determine the original status of the ecosystem, and it is likely that many coastal areas have suffered from the ‘shifting baseline syndrome’ (Pauly 1995, Dayton et al. 1998). Another challenging task in monitoring of benthic communities is to understand and discriminate responses in cases of interacting effects where community responses are likely to be complex and irregular. One attempt to understand underlying patterns and disentangle natural variability and impacts from external factors, is through the study of systematically sampled long-term data (e.g. Southward 1995, Hawkins et al. 2003). In the cases of anthropogenic eutrophication embedded within a climate signal, long-term baseline data with extensive spatial and temporal coverage are strongly needed (Edwards et al. 2006).

Long-term monitoring of soft bottom communities in order to detect effects of external factors has been carried out at several places in the North Sea. The longest time series is from two stations (50 m and 80 m deep) at Northumberland (UK), which have been sampled since the 1970s. During the period there have been changes with approximately ten-year intervals in faunal composition which could be related to climatic factors, production in overlying waters and fishing intensity with various effects in different time periods (Frid et al. 2009a, b). Also in other parts of the North Sea, time-series have documented long-term trends in the benthos, and that faunal variation could be related to e.g. climatic factors, nutrient input, plankton as well as freshwater-runoff (e.g. Tunberg & Nelson 1998, Hagberg & Tunberg 2000, Josefson & Hansen 2003, Reiss et al. 2006). Most studies have focused on patterns in species assemblages, but there is currently an increasing interest in the use of biological traits, which can be defined as the morphological, physiological, phenological or behavioral features of an organism that describe its performance (Violle et al. 2014). Traits are often used as surrogates for ecosystem properties as they have been documented to affect multiple ecosystem functions, and thus traits analyses are increasingly used as means to improve the assessment of marine ecosystem functioning including the understanding of the actual ecological significance of disturbance effects (Oug et al. 2012, Beauchard et al. 2017).

In Norwegian waters, the Norwegian Coastal Monitoring Programme has monitored the environmental status and development in coastal parts of Skagerrak since 1990 (Norderhaug et al. 2011). The programme has regularly collected data for soft bottom communities and shallow subtidal hard bottom communities, as well as for climatic factors, nutrients, particle loading and microalgae in the pelagic. Thus, the programme covers a multitude of environmental and biological parameters from shallow to deeper areas in the Skagerrak and eastern North Sea. The main aim of the programme has been to reveal possible effects of eutrophication and climate change on the coastal ecosystems. It has been an important part of the project to distinguish between the effects from long-distance transported substances and local sources.

Environmental management needs better information about complex ecosystem dynamics (Frid et al. 2005), and about the single and interactive effects of disturbances such as eutrophication and climatic variation on marine ecosystems. The aim of the present work is to examine the development of the coastal soft bottom communities in the Skagerrak within the period 1990-2010 and the influence of eutrophication and climatic variation. Specifically, spatial and temporal changes in water temperature, salinity, nutrients, and suspended particles are related to species richness, diversity, community structure and community functioning. The effects on shallow water hard bottom systems for the same time period have been reported by Norderhaug et al. (2015).

2. MATERIALS AND METHODS

2.1. Sea area characteristics

The Skagerrak is a part of the North Sea situated between the southeast coast of Norway, the southwest coast of Sweden, and the Jutland peninsula of Denmark. It connects the main North Sea and the Kattegat sea area, which leads to the Baltic Sea (Figure 1). It is a hydrodynamically complex area, where water masses from the North Sea and the shallow, brackish Kattegat meet and mix (Figure 1). The coastal water along the Norwegian Skagerrak coast is basically a mixture of two water masses; Atlantic water and freshwater. Most of the freshwater comes from three sources; local runoff to the coast, the Baltic Sea and the large rivers draining to the southern part of the North Sea. These water masses combine to form the Norwegian Coastal Current.

The Coastal Current and thereby Skagerrak receives large regional nutrient inputs from European rivers (Aure & Magnusson 2008). The mean annual freshwater supply to the Skagerrak from the Baltic Sea and the Kattegat is estimated to ca. 215 000 m^3 s^{-1}, and in addition, a large fraction of the 4 500 m^3 s^{-1} of continental river discharge to the North Sea passes through the area (Aure et al. 1998). Particularly water from the German Bight strongly influences the water quality. This water contributes to approximately 75% of nitrate and 40% of phosphate in the Coastal Current, respectively, but in the period 1990-1995, when discharges from European rivers reached a maximum level, the contribution was approximately 83% and 48%, respectively (Aure & Magnusson 2008). Strong management effort has lead to an improvement in the water quality, although the current levels still are considerable higher than during earlier periods (1965-1980) (Norderhaug et al. 2011). Notably, in contrast to declining nutrient concentrations, the concentrations of carbon and nitrogen in seston, dissolved organic nitrogen and the estimated fraction on non-autrophic material have been found to undergo a rapid increase between 1998 and 2000, and have remained at a higher level since (Frigstad et al. 2013). This increase is probably caused by increased inputs of terrestrial-derived, humic material due to an increased freshwater runoff (Frigstad et al. 2013).

2.2. Sampling stations

Two soft bottom stations were positioned within each of three areas; the outer Oslofjord (A), the southeast coast (B), and the southwest coast (C) (Figure 1). In each of the areas A and B, one coast-near shallow (A05 and B05; 50 m depth) and one outer deep (A36; 360 m and B35; 350 m) soft bottom station was sampled (Figure 1). Area C also had one deep station (C38; 380 m), while the other station was placed in intermediate depth inside a fjord (C16; 160 m). Originally, the program was composed of more stations than the present six, and was also supposed to include fjord environments, which is the reason why station C16 apparently not accords with the other stations.

Hydrophysical and hydrochemical parameters were collected from four pelagic stations located within the three areas (one in A, two in B, and one in C), at a maximum distance of 30.6 km from the benthic stations (Figure 1). The benthic and pelagic station positioning was designed according to circulation and stratification patterns in the areas, and the pelagic stations are considered to represent the water in the area of the biological stations well (NIVA 2002). At the pelagic stations, the water column was sampled from the surface down to the seabed at standard intervals (0, 5, 10, 20, 30, 50, 100, 125, 150, 200, 250, 300 and 400 m, with some adjustments to ensure sampling at 5 m above the seabed). The pelagic station Oslofjord 1 (0-440 m) supported the two A-stations; Arendal 3 (0-240 m) supported B35, Arendal 2 (0-50 m) supported B05, and Lista (0-300 m) supported stations C38 and C16. Due to logistic and financial reasons, the position of the pelagic station in the outer Oslofjord (Oslofjord 1) was slightly adjusted three times during the monitoring period. It was assumed that these adjustments did not influence the results significantly.

2.3. Sampling and processing

2.3.1. Soft bottom fauna

The six benthos stations were sampled with a 0.1 m^2 Day or van Veen grab in May or June each year from 1990 to 2010, and fauna was sieved on a 1 mm screen. The field work and processing were performed according to guidelines for quantitative sampling and sample processing of marine soft-bottom macrofauna (NS-EN ISO 16665:2013). At each sampling occasion, either four or eight grabs were sampled, but for the purpose of the present analyses four grabs (in the case of eight, the first four) were used to make observations comparable. All specimens were identified to species or lowest taxon possible. The species matrix of the faunal data consisted of more than 140,000 individuals belonging to 531 taxa. Before analyses, abundances were calculated as average values per 0.1 m^2 for each station and sampling occasion. The raw taxon data matrix was inspected for inconsistencies in the identifications including changes in taxonomy. Despite twenty years of data, very few persons have been involved in the identification and care has been taken to transfer competence at change of personnel, which reduces the chance of inconsistency in the species list.

2.3.1. Environmental variables

Samples for percent sediment fine fraction (i.e. the pelite content measured as % particles < 0.063 mm) and mg/g total organic carbon (TOC) were collected at the soft bottom stations at each sampling occasion. Fine fraction was determined by wet sieving, while carbon was determined using a CHN (i.e. Carbon, Hydrogen, and Nitrogen) analyser after removal of inorganic carbons by acidification. According to Norwegian monitoring practice (e.g. Water Directive Guide

02:2013), the measured (m) TOC content was normalized (n) to adjust for varying sediment fine fraction (FF):

$$TOC_n(mg/g) = TOC_m(mg/g) + 18(1 - FF)$$

Temperature (T) and salinity (Sal) in the water masses were sampled monthly or bi-monthly at the pelagic stations (Figure 1) with the use of CTD (i.e. Conductivity, Temperature and Depth instrument). Simultaneously, water samples were taken and analysed for hydrochemical and plankton contents that resulted in the following variables: total phosphorus (TotP), phosphate (PO_4^3, denoted PO_4), total nitrogen (TotN), nitrate + nitrite (NO_3^-+NO_2^-, denoted NO_3+NO_2), particulate organic carbon (POC) and nitrogen (PON) and chlorophyll a (Chla). The sampling procedure was performed according to OSPAR Guidelines for the Joint Assessment and Monitoring Programme (JAMP, OSPAR 2009) as well as ICES technical manuals and Guidance on sampling from marine waters (NS-ISO 5667-9:1992).

2.4. Data analyses

Temporal changes in species richness and diversity were assessed in relation to environmental variables using Generalized Additive Models (GAM) and regression analyses. Spatial and temporal patterns in species communities and functional attributes were analysed using non-metric multidimensional scaling (nMDS: community structure) and principal coordinate analysis (PCoA: community functioning). Relationships between species communities and environmental variables were examined using distance based redundancy analysis (db-RDA). As far as possible, the GAM analyses on univariate measures (S, H') and the nMDS and db-RDA on the multivariate species data were designed in comparable ways in order to assess if the same environmental variables influenced both species richness, diversity and composition of the species communities.

2.4.1. Environmental variables

A total of 48 environmental variables representing sediment conditions, climate, nutrient concentrations and topography (depth and longitude) were designated for the analyses of fauna-environment relationships. Sediment conditions were represented by the measured values for pelite content and TOC (normalised). From the hydrophysical and hydrochemical measurements, variables for temperature, salinity, nutrients (TotP, PO_4, TotN, NO_3+NO_2), particulate organic matter (POC, PON, POP) and chlorophyll a (Chla) were derived. Monthly averages were calculated and used as separate variables for July (previous year), October (previous year), January, and April to represent summer, autumn, winter and spring conditions prior to the time of biological sampling (May/June). For temperature, also the maximum values observed during the last twelve months before the time of biological sampling were used. Values were either taken from the depth closest to the seabed reflecting the ambient conditions for the benthos (e.g. temperature and salinity) or taken from the upper water column (0-30 m) in order to reflect the algal production (e.g. production-related variables).

In addition to measured parameters, station depth, position (latitude and longitude) and the North Atlantic Oscillation (NAO) index were entered among the environmental variables. NAO is a measure of the strength of the sea-level air pressure gradient between Iceland and the Azores (Bjerknes 1964). In the present study, the winter-based (December through February) NAO was used. This variable was used in the analyses both for the same year as the biological sampling (denoted NAO) and as a time-lagged variable, i.e. NAO for the previous year (denoted NAO_{prev}).

2.4.2. Variable selection

Due to inconsistency in the water mass sampling (changes in sampling program, technical problems, bad weather etc.), not all environmental variables were sampled for all stations at all times. For univariable analyses (i.e. one predictor at a time) this is technically not a problem, but for model selection using GAM and ordination analyses (see below) that require no missing data for any of the variables, several variables and/or samples had to be omitted to obtain complete data matrices. The variable selection was thus a trade-off between maximising the number of samples (i.e. few variables) and including as many variables as possible (i.e. smaller sample size). This resulted in a compromise where the following variables was excluded from GAM and ordination analyses: POC, PON and Chla for all four seasons and all environmental variables for the month of July (T, Sal, TotP, PO_4, TotN, NO_3+NO_2).

After exclusion of incomplete environmental variables, the number was reduced to 23 variables available for model selection by GAM and ordination analyses. This number was still high and needed to be reduced for the GAM modelling of species richness and diversity to reduce the risk of model overfitting and to reduce computational time in the model selection procedure. Therefore, a subsequent *a priori* variable selection procedure was carried out before the actual analyses to identify highly correlated variables. The selection was performed based on an inspection of the concurvity (the nonparametric analogue of collinearity, Ramsay et al. 2003) matrix between all remaining, full-length environmental variables. The selection was done in a sequential way where the one variable of a pair of the highest correlated (i.e. with highest concurvity values according to the type "estimate" in the *mgcv* library, see below) variables, that also correlates most with other variables, was removed. A new concurvity matrix was then made after each removal, until a model with 15 variables with concurvity less than or equal to 0,51 was reached. This was found as a reasonable compromise between too few and too correlated predictors (Table 1). A total of 15 largely uncorrelated environmental variables were then subject to the analyses. A correlation matrix (not concurvity, since concurvity estimates are based on a full model including all variables, and such a large model was not possible) including also the excluded variables is available (Supplement 1), which might be useful for considering patterns of correlations between all environmental variables.

The inclusion of the time-lagged environmental variables (i.e. measures from summer and autumn one year prior to the biological sampling) in the analyses of species richness and diversity necessitated the exclusion of faunal 1990 data. This resulted in a sample of 82 observations, as opposed to the 126 observations available for the multivariate analyses (Table 2).

2.4.3. Univariate analyses - analysis of species richness and diversity

For each sample, species richness (S) and Shannon-Wiener diversity index (H'$\log_2$) (Shannon & Weaver 1963) were calculated. The diversity index accounts for both abundance and evenness of the species present, i.e. H' increases both with number of species and as the proportion of individuals per species becomes more constant (Gray & Elliott 2009). The average of S and H' over the four samples (i.e. per 0.1 m^2) was used in the analyses for each station and sampling occasion.

Patterns in species richness across stations (beta or turnover diversity) were assessed using Whittaker's beta index. The index was calculated according to the formula $b_w = (S_{tot}/S_{stn}) - 1$ (as cited by Magurran 1988), where S_{tot} is the total number of species collected per sampling occasion, and S_{stn} is the average number of species per station (i.e. per 0.4 m^2). The index measures to which degree the whole investigated area is richer in species than the sampling stations within the area.

All analyses of species richness and diversity at stations (S, H') with relation to the environmental variables were carried out using R version 2.15.1 (R Development Core Team 2012). First, S, H' and all the 48 environmental variables available were tested for possible linear time trends through the study period in univariable (i.e. individual) analyses using the lm function in the R library *stats* (R Development Core Team 2012). Then, relationships between each environmental factor and S and H' were assessed using the function gamm in the library *mgcv* (Wood 2011) for Generalized Additive Mixed Models (Mixed GAM; Zuur et al. 2009). A smoothing parameter (k) of max 3 was chosen for all continuous predictors, to allow for some degree of non-linear effects, but not overfitting the models. Station ID was included as a random factor in the GAMs to account for a potential dependence between observations taken at the same site.

In subsequent analyses combinations of environmental variables for explaining species richness (S) and diversity (H') were tested by model selection using mixed GAM. For this purpose, the reduced dataset consisting of only the 15 preselected environmental variables were used. This dataset consisted of variables that were only weakly correlated and had no missing data to meet the criteria of model selection (Burnham et al. 2011). By the use of the R library *MuMIn* (Barton 2013), several thousand candidate models were tested, using all possible combinations of the 15 environmental predictor variables, and ranked by the use of Akaike Information criterion (AIC_c, Burnham et al. 2011). Due to the limited number of degrees of freedom and the great number of variables, interaction effects were not tested in the model selection procedure. Instead, the potential non-additive effects of eutrophication and climate were analysed after finishing the model selection by including their interaction to the best of candidate models that included the two component variables of the interaction; each interaction in separate models.

Beta diversity was related to environmental variables by linear regression. All variables representing climate and water mass characteristics (nutrients, particulate materials, cholophyll a) were used. In order to maximise the number of variables, data from stn B05 were used and here considered to reflect the major trends in the whole area (42 variables, omitting station position and topography, see Table 2).

2.4.4. Multivariate analyses - analysis of species composition and community functioning

To analyse for similarities in the composition of species communities, non-metric multidimensional scaling (nMDS) was used, based on Bray-Curtis similarity measure. Similarity-calculations were based on fourth-root transformed data. This analysis was performed for the complete biological dataset (i.e. all stations at all years; n = 126), in addition to each station separately. Similarity percentage (SIMPER) analysis (Clarke 1993) was performed to obtain information on changes in species composition during the time-period (1990-1999 vs. 2000-2010). For analysing relationships between species composition and environmental variables, Distance-based Linear Model (DistLM, Anderson 2001) was used. In order to obtain results that could be comparable with the GAM-analyses, the same set of 15 environmental variables and faunal data was used (see Table 2). Final inclusion of predictor variables in the model was based on AIC_c criterium and a stepwise (which includes a forward as well as a backward step) selection procedure. Sequential tests were done using 9999 permutations of residuals under the reduced model. The ordination method of distance-based redundancy analysis (db-RDA) was used to visualise the results. The db-RDA runs an eigen analysis and produces an ordination which is constrained to be a linear combination of the environmental variables responsible for explaining significant portions of the variation within the data cloud. DistLM and the corresponding db-RDA were performed for the reduced data matrix. Also, marginal test was performed in DistLM in order to quantify how much variation each variable explains alone, i.e. ignoring other variables. The multivariate analyses were performed with PRIMER package version 6.1.13 (Clarke and Warwick, 2001).

To analyse for patterns in functional attributes of the species communities, biological trait analysis (BTA) was conducted. Species abundance data were combined with traits data for each species to calculate community weighted means (CWMs or 'trait profiles') expressing the functional composition of the species assemblages (see Bremner et al. 2003, 2006, Oug et al. 2012, 2018, Beauchard et al. 2017). Nine traits representing adult life habit, degree of attachment, mobility, size, body form, sediment dwelling depth, feeding mode, larvae type and sediment reworking were used. These properties are key components of essential functions provided by coastal benthic ecosystems, and are considered to reflect basic ecological aspects of the species, including implications for sediment reworking and community stability. Each trait is divided in a number of categories (2-9) that expresses different states of the trait. The species traits data were extracted from a database held by Norwegian Institute for Water Research (NIVA) where information has been compiled from a broad selection of literature and by consulting experts (Oug et al. 2012), except for sediment reworking where data presented by Queirós et al. (2013) on classification of soft bottom species with regard to bioturbation potential were applied. Species traits were scored according to the 'fuzzy coding' procedure (Chevenet et al. 1994) with values ranging from 0 (= no affinity) to 3 (= dominant) (see Oug et al. 2012, 2018 for further details on trait categories and calculations). The analysis was carried out on a matrix of 187 species by omitting rare species (abundance < 0.0001% of total) and some few more of low abundance lacking traits information. In the resulting matrix the traits information was complete except for larvae type where data were missing for 15% of the species. The analysis was performed with principal coordinate analysis PCoA (= metric MDS based on Euclidean distance for calculation of similarities) in PRIMER package version 6.1.13. Prior to the analysis, species data were fourth-root transformed as for the MDS. The ordination was based on the distances among centroids for each station divided between 1990-1999 and 2000-2010.

3. RESULTS

3.1. General faunal characteristics

Altogether, 531 taxa and more than 140,000 individuals and were recorded in the samples. The species assemblages were generally characterized by small annelids and mollucks. The deep stations A36 in the outer Oslofjord and B35 along the southeast coast were very similar regarding sediment characteristics and faunal composition. The mean sediment fine fraction was as high as 99% at both stations. The fauna was dominated by small bivalves (e.g. *Thyasira equalis* and *Abra nitida*) and annelids (e.g. *Paramphinome jeffreysii, Heteromastus filiformis* and *Tharyx* sp.). The deep station C38 at the southwest coast had coarser sediment, with a fine fraction of 76%. This station was mainly dominated by annelids (e.g. *Myriochele heeri, Galathowenia oculata*), brittle stars (e.g. *Amphilepis norvegica*) as well as the ostracode *Philomedes lilljeborgi*. The shallow station A05 in the outer Oslofjord had a sediment fine fraction of 63%, and a fauna consisting mainly of annelids (*H. filiformis, Chaetozone setosa* and *Prionospio fallax*), Nemertea and brittle stars (e.g. *Amphiura chiajei*). The sediment was finer at B05 at the southeast coast, with a mean fine fraction of 87%, despite its shallow location. Here, the fauna was dominated by annelids (e.g. *Diplocirrus glaucus* and *C. setosa*), Nemertini, gastropods (e.g. *Hyala vitrea*) and bivalves (e.g. *Ennucula tenuis*). Station C16 at intermediate depth at the southwest coast had a sediment fine fraction as high as 90%, and annelids (e.g. *H. filiformis, Spiophanes kroyeri* and *P. jeffreysii*) and small bivalves (*T. equalis* and *Kelliella miliaris*) dominated the fauna.

In the MDS-ordination of all stations (Figure 2), the samples were mainly clustered according to station and depth, although C38 also seemed somewhat different from the others (A36, B35, and C16). Station C16 showed the largest variation during the period. Notably, the samples from C16 in 2009 and A05 in 1991 and 2010 were separated from the main groups, but except from this all stations more or less kept their identity throughout the monitoring period.

The analysis of community functioning revealed a main grouping based on station and depth, roughly similar to the analysis of community structure (Figure 3). The horizontal axis largely reflects a geographical gradient, whereas the vertical axis reflects depth with the deep stations at the bottom of the plot. The functional features that contribute most to the ordination pattern were represented by a variety of different traits (life habit, mobility, feeding habit, size, larvae type, degree of attachment and sediment reworking) (Figure 3). The horizontal axis can be interpreted as a gradient from high relative abundance of free-living burrowing and carnivorous species (left; eastern stations) to a general dominance of non-mobile surface and deposit feeders (right; western stations). Larvae type was highly correlated to the vertical axis, with increased dominance by lecithotrophic larvae towards the deep stations and dominance by planktotrophic larvae towards the shallow stations.

3.2. Temporal variation in faunal characteristics

Species richness and diversity varied both among stations and over time during the monitoring period (Figure 4). There was an overall increase in average species richness over time (linear regression: $p=0.02$, $R^2=0.16$), but not in diversity ($p=0.15$, $R^2=0.07$). The total species richness in the sampling area increased gradually (linear regression: $p=0.003$, $R^2=0.37$). The beta diversity showed a cyclic pattern with periods with higher diversity (generally more species across stations) separated by periods with lower diversity (Figure 4).

The species composition changed gradually at all stations during the monitoring period (Figure 5). The trend was more or less the same for all stations with samples from the 1990s placed towards the left side of the plot and the samples from the 2000s towards the right side. To identify the species showing the largest changes, a SIMPER-analysis was performed (Table 3). For instance, the annelids *Heteromastus filiformis*, *Paramphinome jeffreysii* and *Tharyx* sp. showed marked reductions from the 1990s to the 2000s, while the annelid *Myriochele heeri* and the bivalves *Thyasira equalis* and *Abra nitida* increased in abundance. Notably, typically increasing species were shell-bearing molluscs and tube-building annelids, whereas decreasing species were free-living annelids and nemerteans.

Temporal changes were also seen in the analysis of community functioning (Figure 3). The increase of shell-bearing molluscs and tube-building annelids and the decrease of free-living annelids were reflected in the increase of attachment and permanent tubes and the decrease of mobility, displayed on the first axis. The changes were most apparent at the deep stations (B35, C38), where non-mobile surface and deep deposit feeders increased from the 1990s to the 2000s. At the more shallow stations (A05, B05), suspension feeders with planktonic larvae appeared to increase, whereas unattached subsurface deposit feeders decreased in the same period.

3.3. Temporal variation in environmental variables

During the monitoring period, the climate in Skagerrak and North Sea was generally mild, and NAO indices were positive or close to zero during winter, with relatively high temperatures and more than average precipitation in most years (Supplement 2). However, in 1996, 2010 and partly 2001, the winter weather was cold and dry, resulting in strongly negative NAO indices. January temperatures increased steadily (linear regression: $p<0.0001$) during the monitoring period, while the other temperature variables did not show the same linear trend (Supplement 2). Regarding nutrient concentrations, a trend with decreasing April concentrations was evident, which was significant for PO_{4Apr} and $TotN_{Apr}$, and close to significant for NO_3+NO_{2Apr} and $TotP_{Apr}$. A significant linear trend with increasing concentration throughout the time-period was found for $TotN_{Jul}$, however, a sudden increase took place in the late 1990s, and a linear trend does not describe the pattern well. A similar increase was recorded for $Chla_{Jul}$ towards the end of 2000s. In general, Chla had some extreme values in certain years, and general trends were not obvious (Supplement 2).

3.4. Environmental effects on species richness and diversity

The response of species richness (S) and diversity (H') to all selected environmental variables were first analysed in individual, univariable (i.e. one single environmental variable in each model) Mixed GAMs, see Figure 6 (only relations with $p<0.1$ are shown). Regarding diversity (H'), no variables were significant, thus no plots are presented from these analyses. Species richness responded significantly to the pelite content and NAO (for the previous year) and to various variables related to the nutrient content of the water column ($TotN_{Jan}$, $TotP_{Apr}$, PO_{4Apr}, $TotN_{Apr}$, NO_3+NO_{2Apr} and $TotN_{Oct}$). There was weak evidence for increasing species richness with increasing temperature in January ($p=0.060$, Figure 6). In general, lower species richness was found after a spring with high concentrations of nutrients, while the opposite was true for autumn conditions the previous year as $TotN_{Oct}$ was associated with an increase in species richness. A predominantly positive response was also observed for low and medium levels of $TotN_{Jan}$, however a negative, but uncertain, effect was also found at high levels of TotN (Figure 6).

In the Mixed GAM analyses more than 250,000 candidate models consisting of all possible combinations of the 15 selected environmental variables were tested for effects on both species richness and diversity during the model selection procedure. Models were then ranked according to their AICc values, with the most parsimonious models at top. The analysis of environmental factors on species richness was generally much more convincing than the one for diversity. In fact, based on AICc values, none of the candidate models tested explained the variation in diversity better than the null model (i.e. no environmental variables included) with $\Delta AICc = 3.4$

towards the second best model including only $TotN_{Oct}$. Nor did any of the models including the interaction between eutrophication and climate rank higher than this (best interaction model was the one between NO_{3Apr} and NAO with ΔAICc=14.3 towards the null model). These results also correspond well with the fact that no variables were significant for H' in the uni-variable mixed GAMs presented above.

For species richness, on the other hand, nine different candidate models were regarded as equally good, since their ΔAICc were less than 2 (Burnham et al. 2011). These nine models included four or five variables, represented by 11 of the 15 environmental variables tested. Only NO_3+NO_{2Apr}, T_{Apr}, TOC, and $TotP_{Jan}$ were not included in any of these models. Further, when checking the AICc-values for the interaction models, most of them were considerably better than their additive counterpart.

To be able to compare the relative importance of the environmental variables against each other, a set of the best models was examined. The models included most of the variables tested, but still had sufficient support from the data. A ΔAICc level of <7 was thus chosen (Burnham et al. 2011), resulting in a set of 35 and 10 models of species richness and diversity, respectively (Table 4). For species richness, the most important variable was depth, with a Relative Importance Value (RIV, ranging from 0 to 1) of 0.996 (meaning it was included in almost all of the 35 models considered). Depth was followed by the pelite content (RIV=0.69), NO_3+NO_{2Jan} (RIV=0.59), $TotP_{Apr}$ (RIV=0.36), T_{Jan} (RIV=0.34), $TotN_{Oct}$ (RIV=0.18), NAO_{prev} (RIV=0.17), and longitude (RIV=0.07). Although the importance values were far lower for diversity than for species richness, it can be worth noting that $TotN_{Oct}$ (RIV=0.11) and depth (RIV=0.07) were ranked as the most important variables; the rest was only 0.04 or less. Model averaging (Burnham and Anderson 2002) of the 35 best models of species richness and the 10 best models of diversity (H') resulted in models explaining 56% (R^2=0.56) and 5% (R^2=0.049) of the variation of species richness and diversity, respectively.

Due to the limited number of degrees of freedom, interactions were not included in the model selection procedure. Instead, each possible variable combination of eutrophication and climate was included as interactions to the best of the candidate models that included the two component variables of the interaction. In the case of species richness, models with an interaction generally performed better than models without, and in fact all of the 35 models with ΔAICc<7 included an interaction. Also for diversity, the interaction models ranked high (from rank 14 and further), although no interaction models were among the 10 best models with ΔAICc<7.

For beta diversity, there was a significant ($p < 0.05$) relationship for five variables related to temperature, nutrients and chlorophyll in July the previous year (positive for T_{Jul_prev}, POC_{Jul_prev}, PON_{Jul_prev}, $Chla_{Jul\_prev}$; negative for $PO4P_{Jul\_prev}$). NAO, temperature in January and salinity in January (all positive) were close to significant ($p \leq 0.1$).

3.5. Environmental effects on changes in fauna composition

Faunal community composition responses to environmental variables were examined with DistLM (Table 5). Of the 15 environmental variables examined, 7 were identified as significant in the sequential test, and these variables collectively accounted for 55% of the variance in the fauna. Depth, longitude, pelite, TOC, T_{Jan}, T_{Apr} and NAO_{prev} were identified as significant variables for the community composition, while NO_3+NO_{2Apr} and $TotN_{Jan}$ were close to significant ($p<0.077$). In the marginal test, where each variable is considered alone, 12 of the 15 variables were significant.

In the corresponding db-RDA plot (Figure 7 a and b), the samples were grouped according to stations on the two first axes, as in the MDS-ordination. The first axis was mainly correlated to depth, while the second axis mainly to sediment pelite content and longitude, thus these three variables were the main descriptors for the variation between stations. The third axis was mainly correlated to longitude, TOC, T_{Jan} and T_{Apr}. While depth and longitude are station-specific variables, T_{Jan} and T_{Apr} vary through time. Altogether, the first three RDA-axes explained 86% of the fitted variation, and 51% of the total variation of the multivariate community data. All of the RDA-axes together explained 100% of the fitted variation and 60% of the total variation.

4. DISCUSSION

4.1. Patterns in community composition and functional traits

Soft bottom communities and hydrochemical parameters have been monitored through a 20-year period along the Skagerrak coast. Not unexpected, the six monitoring stations differed with regard to species composition, but the analyses showed that all stations kept their identity during the monitoring period, evidenced by the analyses of community structure (Figure 2) as well as functional features (Figure 3) and relation to environmental variables (Figure 7). During the monitoring period, there were consistent but more or less parallel temporal changes in the species composition and functional features across the stations (Figures 5 and 7). Essentially, these results answer to one of the fundamental questions posed at the onset of the Norwegian Coastal Monitoring Programme; whether the three areas (A, B, C) were differently influenced by local sources, e.g. in eutrophication and fresh-water runoff, or were more influenced by large-scale changes in the Skagerrak water masses including long-transported nutrient components from the southern North Sea. The parallel changes at the stations clearly indicate that large-scale changes were the most important.

It appeared that the species composition had undergone only moderate changes in coast-near areas of Skagerrak during the investigated period. Another study from the central North Sea covering the years 1986 and 2000 suggests that benthos has not exhibited any large-scale changes (Kröncke et al. 2011). Other studies from approximately the same time period as this study report gradual changes in species composition over time in the North Sea (e.g. Rees et al. 2006, Reiss et al. 2006, Frid et al. 2009a, b). Notably, the deep stations in the present study, that are far deeper than other North Sea long-term monitoring sites, also underwent gradual changes at about the same scale during the study period.

A significant increase in species richness was recorded through the monitoring period from 1990 to 2010, with especially low richness the two first monitoring years (1990 and 1991). A similar, but not significant, positive trend was also observed for diversity. It may be noted that 1990 and 1991 were placed in the periphery in the ordination plots of several stations, indicating that these years also were different from the following years regarding species composition. These findings correspond well with patterns of species richness and total abundance in the western North Sea, where Frid et al. (2009a, b) observed a change in the fauna around 1991, which they interpreted as a benthic, lagged response of the "regime shift" in the North Sea plankton community. An alternative, or supplementary explanation for the changes observed in Skagerrak, is that the pattern might be related to a recovery phase after the bloom of the toxic algae *Prymnesium polylepis* (syn. *Chrysochromulina polylepis*). In 1988 an extensive bloom of this toxic flagellate occurred over much of the Skagerrak. Although the main concern of this alga was its effect on littoral wild fish and farmed fish, also the soft bottom fauna was affected (Olsgard 1993). At an impacted area in the western part of Skagerrak (ca. 34 km northwest of station C38), there was a documented clear switch in species composition immediately following the bloom, and a tendency of the fauna to return to the pre-bloom communities one to two years after the event (Olsgard 1993). However, at the most severely affected stations examined by Olsgard, effects appeared to still be present after three years (Gjøsæter et al. 2000).

The analysis of community functioning (Figure 3) revealed that e.g. "suspension feeding" was a more important feature at the shallow stations than at the deeper stations. Presumably the shallow stations are more exposed to bottom currents and suspended particles in the water, which the suspension feeders may benefit on. Larvae type was also highly correlated to depth, with increased occurrence of lecithotrophic larvae, i.e. larvae with short or no pelagic stage, towards the deep stations and increase of planktotrophic larvae towards the shallow stations. This finding may again relate to food availability; as planktonic larvae depend on feeding and growing in the plankton, they obtain more nutrients in shallow than in deeper water (Thorson, 1950). In addition to depth, there was a geographical gradient in the functional traits. Towards the outer part of Skagerrak, there was a larger occurrence of surface and deep deposit feeders, also typically with low mobility.

The small annelids *Heteromastus filiformis*, *Paramphinome jeffreysii* and *Tharyx* sp. showed marked reductions in abundance from the 1990s to 2000s (Table 3). These taxa are often recorded in high densities in organically or otherwise disturbed sediments (e.g. Pearson & Rosenberg 1978, Borja et al 2000). On the other hand, the tube-building annelids *Myriochele heeri* and *Galathowenia oculata* and the bivalve *Abra nitida* increased in abundance (Table 3). Although these species may thrive in slightly organically enriched or physically disturbed sediments, they are usually not present in highly disturbed environments (e.g. Holte & Gulliksen 1998, Borja et al 2000). Furthermore, shell-bearing molluscs and tube-building annelids were among the increasing species, while free-living annelids and nemerteans were decreasing. Generally, larger, tube-building species are more sensitive towards disturbances than free-living, smaller species (e.g. Pearson & Rosenberg 1978, Oug et al. 2012). In total, the change in species richness and species composition observed suggests an improvement of the soft bottom benthos during the study period.

4.2. Environmental variables and patterns in species assemblages

The underlying mechanisms causing spatial gradients and changes with time in species communities may include numerous environmental factors and biotic relationships (Gray & Elliot 2009). Several relationships are well described, whereas others are complex, and not well understood. In the present study, a set of environmental variables was designated for four main relationship groups; location and topography (depth, longitude), sediment conditions (pelite, TOC), climate (temperature, NAO) and food supply (nutrient levels; assumed to reflect the pelagic production). Variables for location and topography, and to some extent sediments, mostly represent differences between the sampling stations, whereas variables for climate and nutrients represent time-dependent environmental changes.

The analyses showed that environmental variables could be related both to species richness and species composition. No relationships were detected for diversity (H'), however. The reason is not clear, but the composite structure of H', with one part based on species richness and the other on equitability, may complicate the relationships. For instance, simultaneous changes in number of species and individuals may not necessarily affect H' (Gray & Elliott, 2009).

Environmental variables from all four main relationship groups were significantly related to faunal patterns. Variables representing basic station 'properties' such as depth, location and sediment grain size (pelite) accounted for the larger fractions of variance in species composition (DistLM-analysis) and ranked among the most important for species richness (mixed GAM). Basically, the strength of these variables supports the intended design of the monitoring programme to include sampling sites with different environmental conditions. Variables related to climate and nutrient loading were less strongly, though significantly related to the faunal patterns. This finding suggests that the faunal variation at the various stations could be associated with measurable changes in environmental parameters.

4.2.1. Topography and sediment conditions

Depth and sediment characteristics are well-known descriptors for soft-bottom fauna (e.g. Ellingsen 2002, Gray & Elliott 2009). Depth is, however, less important as a factor *per se*, but rather represents several factors that vary with depth and determine the basic conditions for the fauna, for instance bottom currents, temperature, supply of food and quality of organic material (Oug 1998, Goginaa et al. 2010, McCallumc et al. 2010). It may vary to which degree these factors are characterized among other environmental variables that are used in the analysis. In both the variable selection in DistLM-analysis and the GAM modelling of species richness, depth ranked at the top possibly because it summarises the effects of several important factors. Grain size may also act as a surrogate variable as it reflects e.g. sedimentation regime, available organic matter, oxygen penetration and sediment stability (e.g. Gray & Elliott 2009). Content of organic carbon (TOC) was significant for species composition, but did not add much to explain variation in species richness. TOC also lumps various conditions by consisting of material of different origins, and in various stages of decomposition (Oug 1998). Longitude scored high in DistLM, but not when it came to species richness. The importance of longitude may reflect changes in faunal composition from inner to outer parts of Skagerrak. This could be a consequence of large-scale topography-dependent factors that regulate species distributions, such as recruitment and larval transport in major current systems.

4.2.2. Trends in climate and nutrients

Several climate and nutrient related variables were identified as significant for species richness and species composition. For the study area as a whole, it seemed that variation in the total species richness expressed by beta-diversity was related to temperature, particulate material and chlorophyll a in the water masses the year previous to the sampling ($\text{July}_{\text{\_prev}}$). Possibly, this may reflect that supply of larvae into Skagerrak and recruitment to the benthic communities increased in years with relatively high temperatures and summer phytoplankton biomass. At station level, the most distinct relationships were observed for winter and spring measurements of temperature and nutrients, i.e. measurements taken 2-5 months before the faunal samples. In particular, temperature in January (T_{Jan}) was the first of the climate and nutrient variables to be selected in the DistLM analyses and ranked high in importance in the GAMM modelling. It may be a rather complex matter, however, to indicate which relationships were the most influential, considering that many variables were excluded from analysis because of missing data, and several variables were omitted due to high inter-correlations. Regrettably, all variables from the month of July the year before sampling had to be omitted from the analyses at stations. The results, however, indicate that the conditions in the water masses in the previous summer, and during winter and spring influences the development of the benthic species communities. It may be noted that the climate variable NAO for the previous year (winter) also was found to be important. This variable may catch a different and more delayed effect on the fauna than the monthly averaged temperature and nutrients variables.

Generally, species richness increased with reduced nutrient concentrations in spring (PO_{4Apr}, $TotP_{Apr}$, NO_3+NO_{2Apr} and $TotN_{Apr}$). Direct cause and effect relationships are not possible to assess from the present study with no information on organic fluxes to the bottom, but the correlations may represent rather general faunal changes to variations in nutrient enrichment. Nutrients in April showed a decreasing trend during the study period from rather high concentrations in the 1990s to lower concentrations towards 2010. This decrease is in accordance with the general trend in coastal waters in Skagerrak (e.g. Norderhaug et al. 2011, Frigstad et al. 2013) and other coastal regions of the North Sea (e.g. Carstensen et al. 2006, van Beusenkom et al. 2008, Voss et al. 2011). The reduced winter and spring concentrations have been interpreted as documentation of a reduced current-transported input of nutrients to the Skagerrak from the southern North Sea (Aure & Magnusson 2008, Vermaat et al. 2008). The decreasing concentrations co-occurred with the faunal shift from small free-living and tolerant annelids to higher dominance of more sensitive small molluscs and tube-building annelids. Thus, the faunal changes could possibly be interpreted as a response to reduced eutrophication, particularly since several of the declining species are generally stimulated by moderate enrichment (see e.g. Pearson & Rosenberg 1978). This is further supported by the concurrent studies of pelagic microalgae in the Norwegian Coastal monitoring programme showing a considerable shift after 2001, with lower biomass and an altered species composition from 2002 until today compared with the period 1994-2001 (Trannum et al. 2012). Also for zooplankton large changes have been observed, e.g. a substantial reduction in *Oithona* spp. and *Paracalanus/Pseudocalanus* spp. (Johannessen et al. 2011). Changes in primary production and the pelagic food web structure may certainly have consequences for the food transport to the bottom, but the processes and links in the pelagic systems involved and the amount and quality of nutrient matters that in the end reach the bottom is difficult to ascertain (see e.g. Josefson 1990, Josefson et al. 1993, Salen-Picard et al. 2002, Josefson & Hansen 2003). Pelagic processes will also be influenced by other factors such as weather conditions and climate, complicating the interpretation of faunal changes in relation to nutrient levels.

In contrast to the other nutrients, total nitrogen (TotN) showed a particular season-dependent relationship to species richness. Increasing levels in autumn ($TotN_{Oct}$) and decreasing levels in spring ($TotN_{Apr}$) were both associated with increased species richness, whereas a bell-shaped relationship was found for winter values ($TotN_{Jan}$). Also, $TotN_{Jan}$ was the only nutrient variable which was not significant in the marginal test in DistLM, indicating that there was no clear relationship between this variable alone and the species composition. It may be noted that Norderhaug et al. (2015) found the same bell-shaped response for $TotN_{Jan}$ on species richness on hard bottom. Although macroalgae are directly influenced by nutrients, there may be a consistent pattern, although not necessarily a direct link, between nitrate in winter and species richness on both hard- and soft bottom.

NAO is a descriptor of climate and correlates with broad variations in weather conditions in northern Europe. Several studies from the North Sea and Skagerrak areas have demonstrated relationships between NAO and benthic species communities (Tunberg & Nelson 1998, Hagberg & Tunberg 2000, Rees et al. 2006, Narayanaswamy et al. 2010, Kröncke et al. 2011). It has been found that single species as well as whole communities and functional groups are correlated to changes in NAO (Hagberg et al. 2004). The factors underlying these responses are not fully understood (Reid & Valdés 2011), but what is assumed, is that the influence of meteorological drivers on marine systems is complex, and involves not only influence on temperature and sea currents, but also mediation through plankton and benthic-pelagic coupling that typically produce time-lagged responses (Frid et al. 2009b). In the present study, it is worth noting that NAO for the previous year seemed to be much more important than NAO for the same year, which indeed points to a time-lagged response. In particular, factors affecting timing, amount and quality of organic matter which settles on the sea floor may seem to be important (e.g. Tunberg & Nelson 1998, Pearson & Mannvik 1998, Rabalais et al. 2009, Kröncke et al. 2011). With a high NAO there is larger inflow of warm and nutrient-rich water from the southern North Sea (Hjøllo et al. 2009). Further, weather conditions have a profound influence on freshwater runoff and material transported from land into the sea. In mild and wet winters (high NAO), when precipitation and thereby runoff is high, much plant debris and eroded soil material are transported into the coastal waters. In Swedish waters, a relationship between nutrient transport from land and benthic abundance and biomass has been established, assuming a link through phytoplankton production (Josefson 1990, Tunberg & Nelson 1998).

Interestingly, NAO was not only found to be associated with changes in species composition, but also with species richness, where an increase in NAO (i.e. mild winters) was accompanied by a small, but consistent, decline in species richness the following year. A similar relationship was documented by Rees et al. (2006) for the western North Sea. Rees et al. (2006) suggested that the density and variety of species may be lower in response to warmer winters characterized by westerly airflows, which was a common feature of the weather patterns in the 1990s. Further, as discussed above, if an increase in NAO leads to increased organic matter content in the water-column, a subsequent response of the benthos may take place, albeit with different time lags at different depths. It is worth mentioning that an increase in T_{Jan} was associated with an increase in species richness. This finding may apparently be in contrast to the relationship between NAO and S, but it is important to have in mind that it was NAO_{prev} (i.e. NAO one year before T_{Jan}) which was significant for the patterns in community structure and species richness. Further, as discussed above, NAO is assumed to act through complex and time-lagged rather than direct mechanisms (see also review by Birchenough et al. 2015).

4.2.3. General considerations

Despite the effects of eutrophication in general have been reduced during the last two decades, climate change may counteract some of this positive trend (McQuatters-Gollop et al. 2009, Rabalais et al. 2009). Indeed, nutrient inputs from some Norwegian rivers and aquaculture have increased recently (Skarbøvik et al. 2010). Further, there has been an increase in seston, dissolved organic nitrogen (DON) and non-autotrophic materials (Frigstad et al. 2013) as well as a darkening of coastal waters, partly due to such increased runoff (Aksnes et al. 2009). Thus, there appears to have been a shift towards increasing importance of local discharge sources relative to long-distance sources (Aure & Magnusson 2008, Norderhaug et al. 2015), which is of general concern. The massive reduction of sugar kelp *Saccharina latissima* that took place in the late 1990s in shallow inshore waters, assumed to be a consequence of higher summer temperatures and increased siltation from freshwater runoff (Moy & Christie 2012), may be an early effect on benthic ecosystems. On outer coast however, hard bottom communities are far less affected (Norderhaug et al. 2015). In deeper water, no large-scale ecosystem changes have been observed, but, still, the present study documents that there were significant changes in the soft bottom fauna from the 1990s to the 2000s. This significant, though less dramatic changes in soft bottom fauna reported here, evidence a dampened response in deeper ecosystems. This agrees with the general results from the long-term studies in western North Sea where the soft bottom species communities appear to have undergone decadal shifts more or less coordinated with changes in dominant driving forces (Frid et al. 2009b). Complex mechanisms linking pelagic production and benthos, greater longevity of benthos compared to planktonic organisms, and recruitment dynamics of benthic species may contribute to explain the observed lagged and dampened responses to changes in the pelagic systems (Frid et al. 2009a, b).

Thus, it is evident that there have been modifications of all ecosystem compartments around the year 2000. Frigstad et al. (2013) considered the concurrent changes in nutrients and particulate matter, zooplankton, fish populations and sugar kelp in the coastal waters of Skagerrak as evidence of a regime shift. Such shift also concurs well with an ecosystem shift in the North Sea, evidenced by several studies both for plankton (e.g. Beaugrand 2014) and benthic communities (e.g. Dippner et al. 2010, Kröncke and Reiss, 2010; Kröncke et al. 2013). As pointed out in these studies, the major driver behind the biological regime shift is probably related to a climatic regime shift. Such climatic change will both have direct and indirect effects (see review by Birchenough et al. 2015), where increased runoff from land and terrestrial derived material is hypothesised as one of the most important impact mechanisms for the coastal ecosystems.

A large proportion of the variance in the biological patterns was not explained by the environmental data, which is not uncommon in observational studies. Marine benthic communities are highly complex and respond to a wide range of ecologically structuring processes acting on different scales (Kraufvelin et al. 2011, Buhl-Mortensen et al. 2012), and it is impossible to measure all the relevant parameters involved in these processes. Also the environmental variables, despite seasonal measures, may not have been collected at the right time to capture important peeks in the time-series. In the present study, some of the unexplained variation can probably be attributed to factors that have not been characterized in the present set of environmental variables, e.g. the *Prymnesium polylepis* bloom in 1988 which may have affected the benthic communities. Further, biological controlling factors, causing variances in e.g. recruitment patterns, competition and trophic group amensalism may add to such unexplained variation (Oug 1998). Even at the very local scale there may be patchiness related to topographic and hydrographical differences at the seabed not accounted for (Gundersen et al. 2011), which will appear as stochastic variation in the data. Lastly, there was a slight discrepancy in the sampling design between the soft bottom and pelagic stations, i.e. the samples were taken close to each other, but not at exactly the same location and depth.

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Table 1. Concurvity matrix of the 15 environmental variables included in the model selection using GAM and ordination analyses. Concurvity is the non-parametric analogue of collinearity (Ramsay et al. 2003), and can be interpreted in the same way as a correlation coefficient; the higher values the higher correlation.

	Long	Depth	Pelite	TOC	NAO	NAO_{prev}	T_{Jan}	T_{Apr}	$TotP_{Jan}$	$TotP_{Apr}$	$TotN_{Jan}$	$TotN_{Apr}$	$TotN_{Oct}$	NO_3+NO_{2Jan}
Depth	0.12													
Pelite	0.41	0.01												
TOC	0.13	0.49	0.16											
NAO	0.02	0.00	0.00	0.02										
NAO_{prev}	0.01	0.00	0.02	0.00	0.02									
T_{Jan}	0.12	0.27	0.02	0.08	0.04	0.01								
T_{Apr}	0.27	0.26	0.03	0.17	0.01	0.02	0.22							
$TotP_{Jan}$	0.01	0.23	0.01	0.13	0.06	0.02	0.02	0.05						
$TotP_{Apr}$	0.05	0.27	0.03	0.10	0.10	0.07	0.01	0.23	0.12					
$TotN_{Jan}$	0.01	0.01	0.10	0.03	0.08	0.02	0.05	0.04	0.27	0.01				
$TotN_{Apr}$	0.08	0.05	0.02	0.08	0.02	0.13	0.15	0.08	0.02	0.10	0.05			
$TotN_{Oct}$	0.09	0.40	0.04	0.05	0.00	0.01	0.10	0.19	0.06	0.20	0.00	0.05		
NO_3+NO_{2Jan}	0.11	0.25	0.04	0.13	0.11	0.00	0.01	0.02	0.49	0.10	0.17	0.00	0.16	
NO_3+NO_{2Apr}	0.08	0.16	0.00	0.11	0.04	0.18	0.02	0.29	0.06	0.51	0.00	0.27	0.11	0.07

Table 2. The total dataset of 21 years and six soft bottom stations showing the number of available environmental variables (upper number, max 48) and the number of final selected environmental variables (lower number, max 15), which also sets the limitation for which stations that could be used in the GAM and DistLM analyses.

	Years																				
Stations	90	91	92	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10
Oslofjord																					
A05	38	48	48	30	4	4	30	24	25	4	4	4	4	30	39	30	30	30	38	4	28
	14	15	15	7	4	4	10	10	8	4	4	4	4	11	15	7	7	14	15	4	14
A36	38	48	48	29	4	4	30	24	25	4	4	4	4	26	33	26	26	25	33	4	26
	14	15	15	7	4	4	10	10	8	4	4	4	4	11	15	7	7	14	15	4	14
SE coast																					
B05	38	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48
	14	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15
B35	37	47	48	48	47	48	48	47	46	47	47	47	48	48	46	48	48	48	48	46	44
	14	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15
SW coast																					
C16	20	30	36	34	31	38	40	40	40	46	48	48	48	48	47	48	48	48	48	48	48
	14	15	15	14	14	15	15	15	13	15	15	15	15	15	15	15	15	15	15	15	15
C38	20	30	36	34	29	38	40	40	38	46	48	48	48	45	45	44	46	48	48	47	46
	14	15	15	14	14	15	15	15	13	15	15	15	15	15	15	15	15	15	15	15	15

Table 3. SIMPER-analysis for all stations treated together for the time-categories 1990-1999 vs. 2000-2010, where taxa representing 70% of the difference between the groups are included. Abundance (no. ind/0.1 m^2), trend ("+" denotes increase; "-"denotes decrease), average dissimilarity (AvDis. %) and cumulative average dissimilarity of differences between the groups area also presented.

	Group 1990-1999 Average abundance	Group 2000-2010 Average abundance	Trend	AvDis %	Cumulative AvDis %
Heteromastus filiformis	84.1	42.8	-	17.0	17.0
Paramphinome jeffreysii	37.0	29.5	-	9.4	26.4
Tharyx sp.	24.5	16.0	-	6.4	32.9
Thyasira equalis	15.9	22.9	+	5.8	38.6
Abra nitida	9.0	13.3	+	3.3	41.9
Myriochele heeri	0.4	11.5	+	2.9	44.9
Caulleriella sp.	9.2	8.1	-	2.7	47.5
Chaetozone setosa	9.9	5.3	-	2.6	50.1
Galathowenia oculata	2.4	8.1	+	2.4	52.5
Diplocirrus glaucus	4.3	3.8	-	2.0	54.6
Nemertea indet.	7.1	6.5	-	2.0	56.6
Spiophanes kroyeri	3.1	5.6	+	1.9	58.4
Lumbrineris sp.	7.3	5.2	-	1.8	60.2
Ceratocephale loveni	3.3	5.4	+	1.5	61.7
Ennucula tenuis	1.8	4.9	+	1.5	63.2
Hyala vitrea	0.9	3.0	+	1.3	64.5
Philomedes lilljeborgi	1.2	4.2	+	1.3	65.8
Kelliella miliaris	1.3	3.9	+	1.3	67.1
Prionospio fallax	1.9	3.0	+	1.2	68.3
Amphilepis norvegica	1.9	3.0	+	1.1	69.4

Table 4. Importance table from the Mixed GAM analyses and model selection of species richness (S) and diversity (H'). Variables are ranked according to their relative importance value (RIV) based on all models with ΔAICc<7. RIV ranges between 0 and 1 and increases with its presence in the models considered, which was 35 and 10 for S and H', respectively.

Variables	**RIV (S)**	**Variables**	**RIV (H')**
Depth	1.00	$TotN_{Oct}$	0.11
Pelite	0.69	Depth	0.07
NO_3+NO_{2Jan}	0.59	$TotP_{Apr}$	0.04
$TotP_{Apr}$	0.36	Pelite	0.04
T_{Jan}	0.34	Longitude	0.03
$TotN_{Oct}$	0.18	$TotN_{Jan}$	0.03
NAO_{prev}	0.17	NAO_{prev}	0.03
Longitude	0.07	NO_3+NO_{2Jan}	0.03
NAO	0.05	$TotN_{Apr}$	0.02
$TotN_{Jan}$	0.03	NAO	0.00
NO_3+NO_{2Apr}	0.00	NO_3+NO_{2Apr}	0.00
T_{Apr}	0.00	T_{Apr}	0.00
TOC	0.00	T_{Jan}	0.00
$TotN_{Apr}$	0.00	TOC	0.00
$TotP_{Jan}$	0.00	$TotP_{Jan}$	0.00

Table 5. Results of the DistLM-model, including Sum of squares (SS), Pseudo-F statistic, p-value and proportional and cumulative explained total variance. Significant ($p<0.05$) variables are in bold. Sequential tests explain the cumulative variation attributed to each variable fitted to the model in the order specified, taking previous variables into account. Marginal tests show how much variation each variable explains when considered alone, ignoring other variables.

Sequential test	**SS**	**Pseudo-F**	**p**	**Prop.**	**Cumul.**
Depth	**44874**	**33.59**	**<0.001**	**0.309**	**0.31**
Longitude	**13910**	**11.93**	**<0.001**	**0.096**	**0.41**
Pelite	**7147**	**6.59**	**<0.001**	**0.049**	**0.45**
TOC	**7643**	**7.69**	**<0.001**	**0.053**	**0.51**
T_{Jan}	**3544**	**3.70**	**<0.001**	**0.024**	**0.53**
T_{Apr}	**1901**	**2.01**	**0.006**	**0.013**	**0.55**
NAO_{prev}	**1427**	**1.53**	**0.049**	**0.010**	**0.56**
NO_3+NO_{2Apr}	1388	1.48	0.058	0.010	0.55
$TotN_{Jan}$	1320	1.43	0.077	0.009	0.57
$TotN_{Oct}$	1168	1.27	0.161	0.008	0.58
NAO	1121	1.22	0.195	0.008	0.59
$TotP_{Apr}$	1054	1.15	0.247	0.007	0.60

Marginal test	**SS**	**Pseudo-F**	**p**	**Prop.**
Depth	**44874**	**33.59**	**<0.001**	**0.310**
TOC	**25859**	**16.27**	**<0.001**	**0.180**
T_{Apr}	**23325**	**14.37**	**<0.001**	**0.160**
Longitude	**17533**	**10.31**	**<0.001**	**0.120**
$TotN_{Oct}$	**16755**	**9.79**	**<0.001**	**0.120**
T_{Jan}	**16604**	**9.69**	**<0.001**	**0.110**
$TotP_{Apr}$	**15039**	**8.67**	**<0.001**	**0.100**
NO_3+NO_{2Jan}	**13277**	**7.55**	**<0.001**	**0.092**
Pelite	**11299**	**6.33**	**<0.001**	**0.078**
$TotP_{jan}$	**10000**	**5.55**	**<0.001**	**0.069**
NO_3+NO_{2Apr}	**6914**	**3.75**	**<0.001**	**0.048**
$TotN_{Apr}$	**5908**	**3.18**	**<0.001**	**0.041**
NAO_{prev}	2044	1.07	0.320	0.014
NAO	2041	1.07	0.332	0.014
$TotN_{jan}$	1546	0.81	0.551	0.011

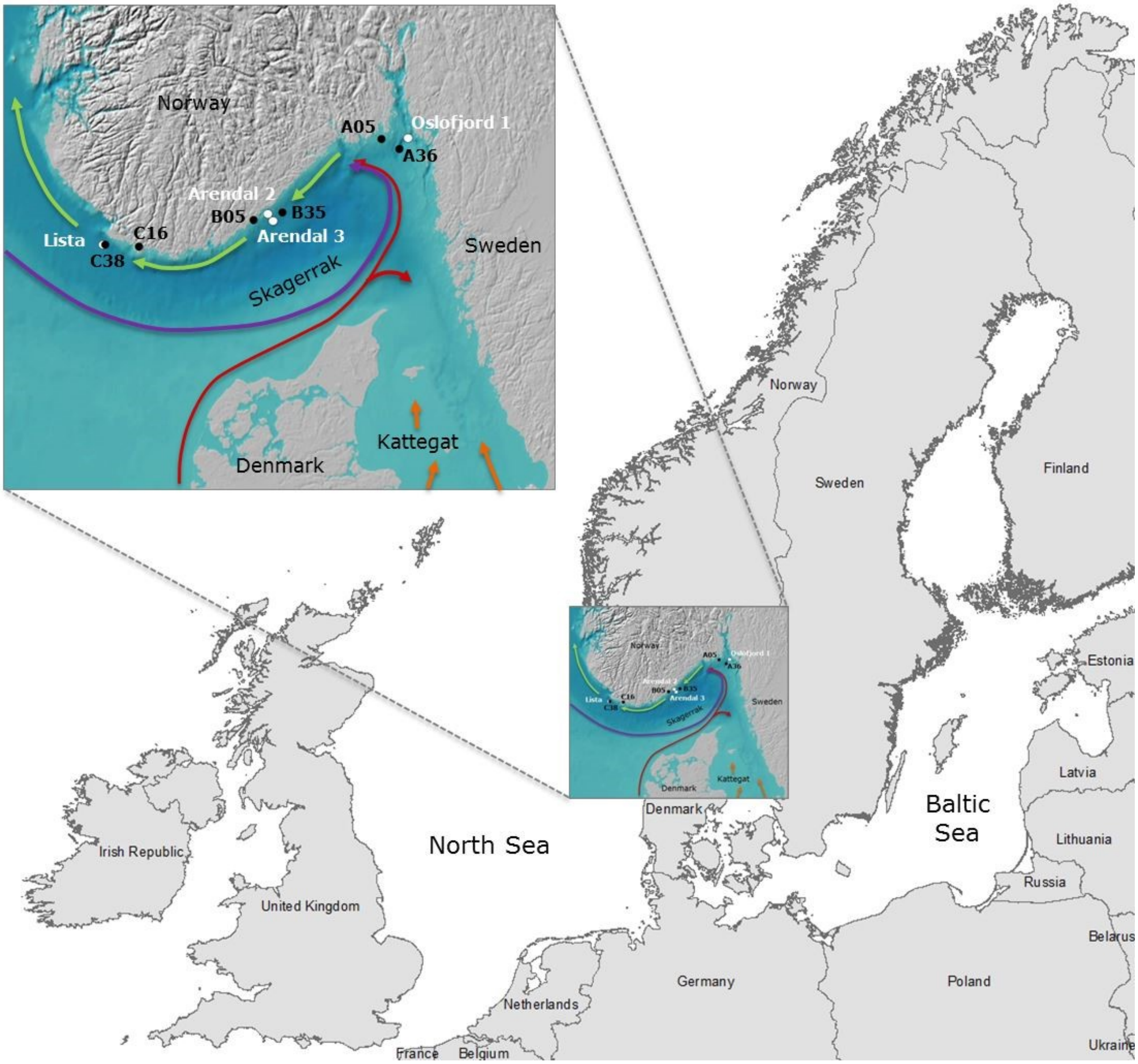


Figure 1. Soft bottom (black dots) and pelagic (hydrophysical and hydrochemical, white dots) stations within the Norwegian Coastal Monitoring Programme. The stations were positioned in three regions: the outer Oslofjord (A), the southeast coast (B), and the southwest coast (C). Main water masses are presented as the Jutland Coastal Current in red, water from Kattegat in orange, Atlantic waters in blue, and the Norwegian Coastal Current in green.

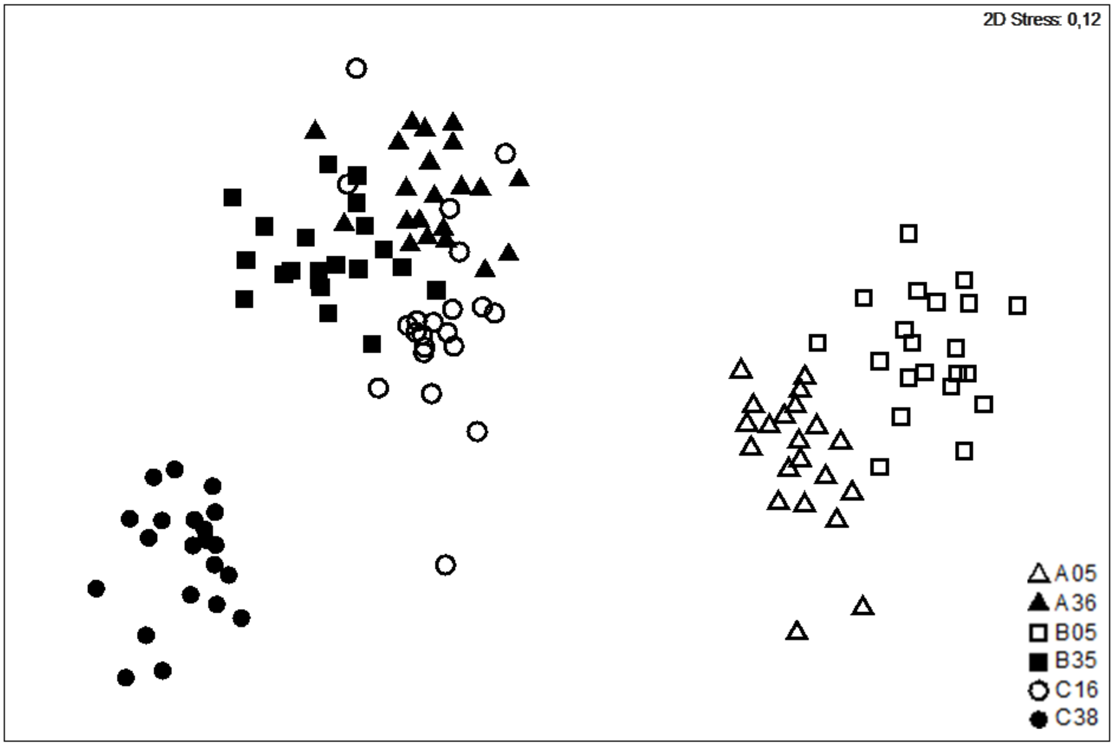


Figure 2. MDS-ordination (based on Bray-Curtis similarity) of soft bottom fauna on the outer coast of South Norway from 1990 to 2010.

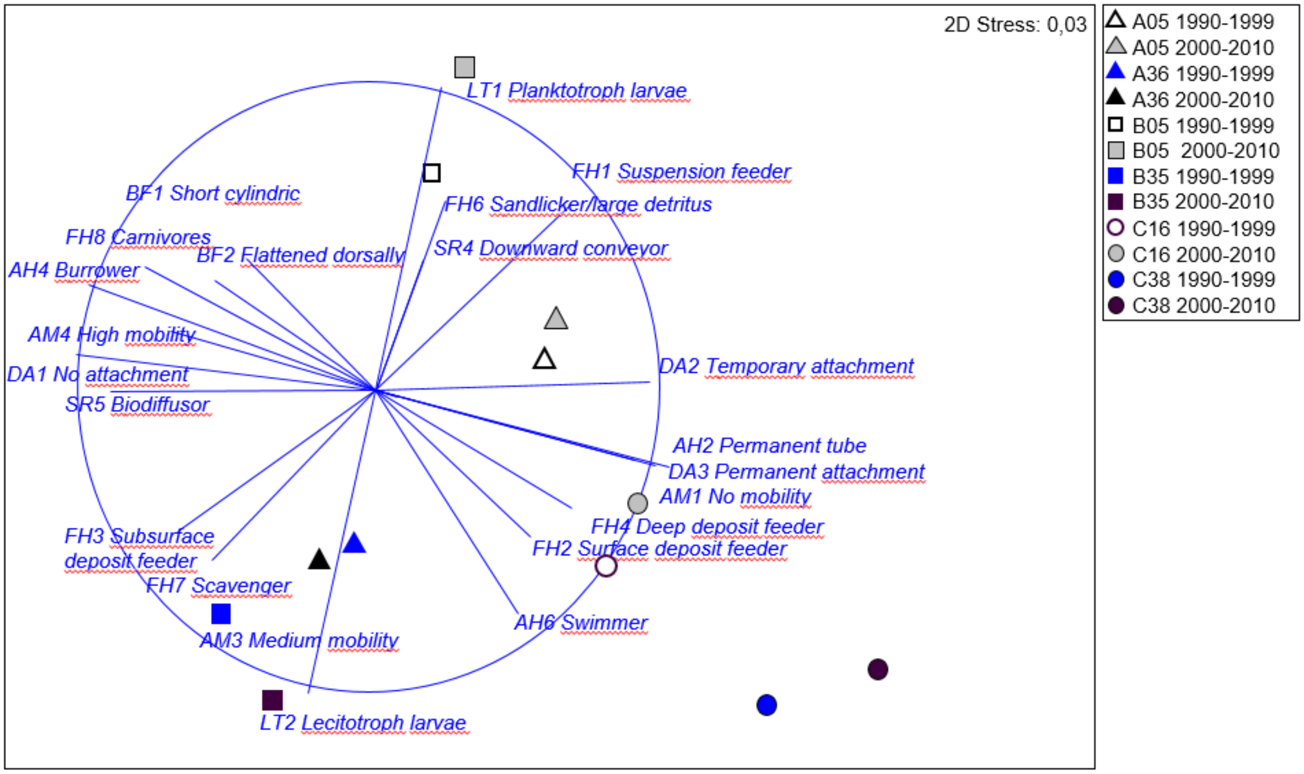


Figure 3. Principal coordinate analysis (PCoA) of species traits of soft bottom fauna on the outer coast of South Norway from 1990 to 2010: biplot of station centroids (divided between 1990-1999 and 2000-2010 to indicate temporal patterns) and trait categories. Trait categories are illustrated as vectors pointing in the direction of maximum increase, long vectors indicate strong trends. For clarity, only traits with high correlation to the axes (Pearson correlation coefficient > 0.6) are shown. These are adult life habit (AH), adult mobility (AM), body form (BF), feeding habit (FH), larvae type (LT), degree of attachment (DA), sediment dwelling depth (SD) and sediment reworking (SR).

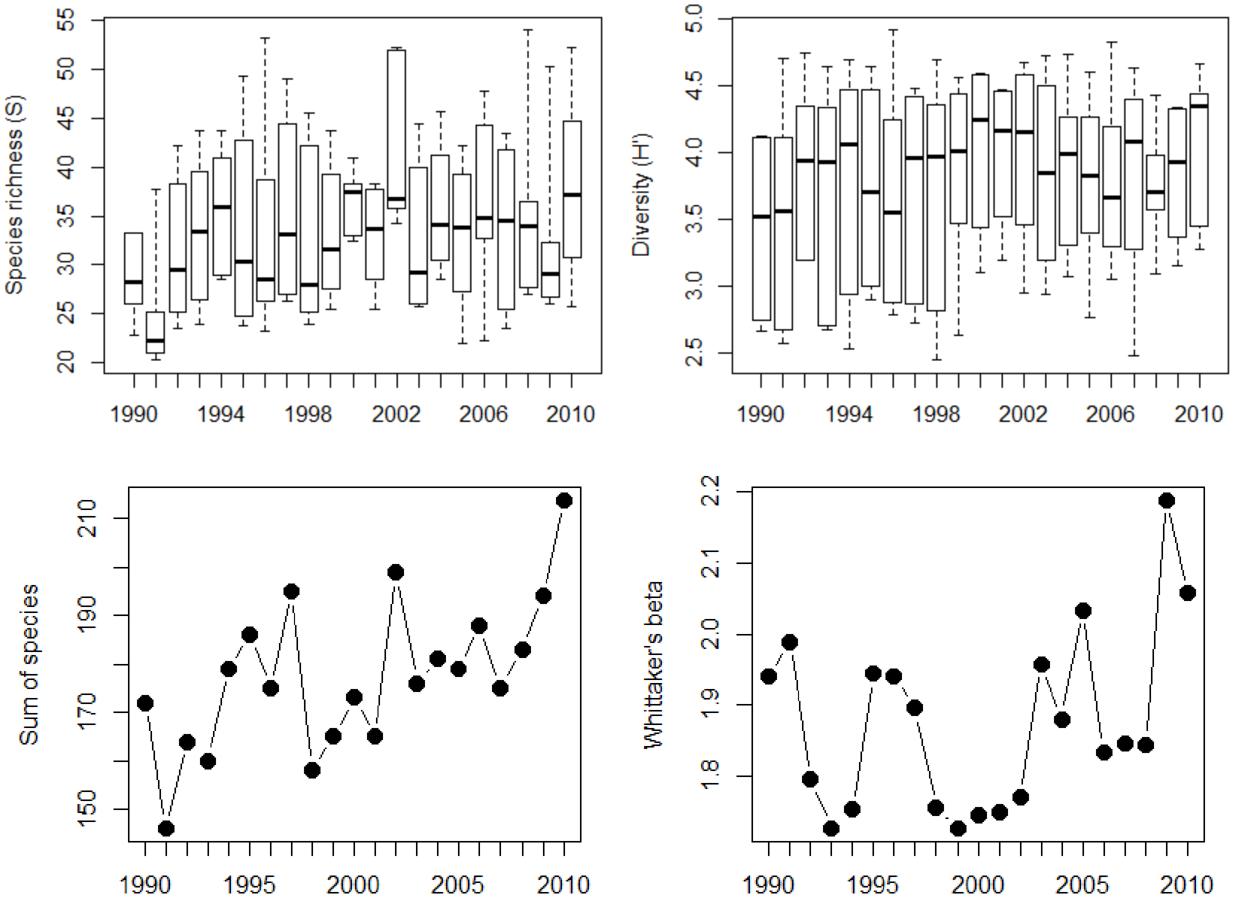


Figure 4. Species richness and diversity of soft bottom fauna on the outer coast of South Norway 1990-2010. Top: Box (interquartile range) and whisker (extends to the most extreme data points) plots of species richness (S) and diversity (Shannon-Wiener index, H') at stations for each sampling occasion (averaged over the stations). Bottom: Total number of species at each sampling occasion and Whittaker's index of beta (turnover) diversity.

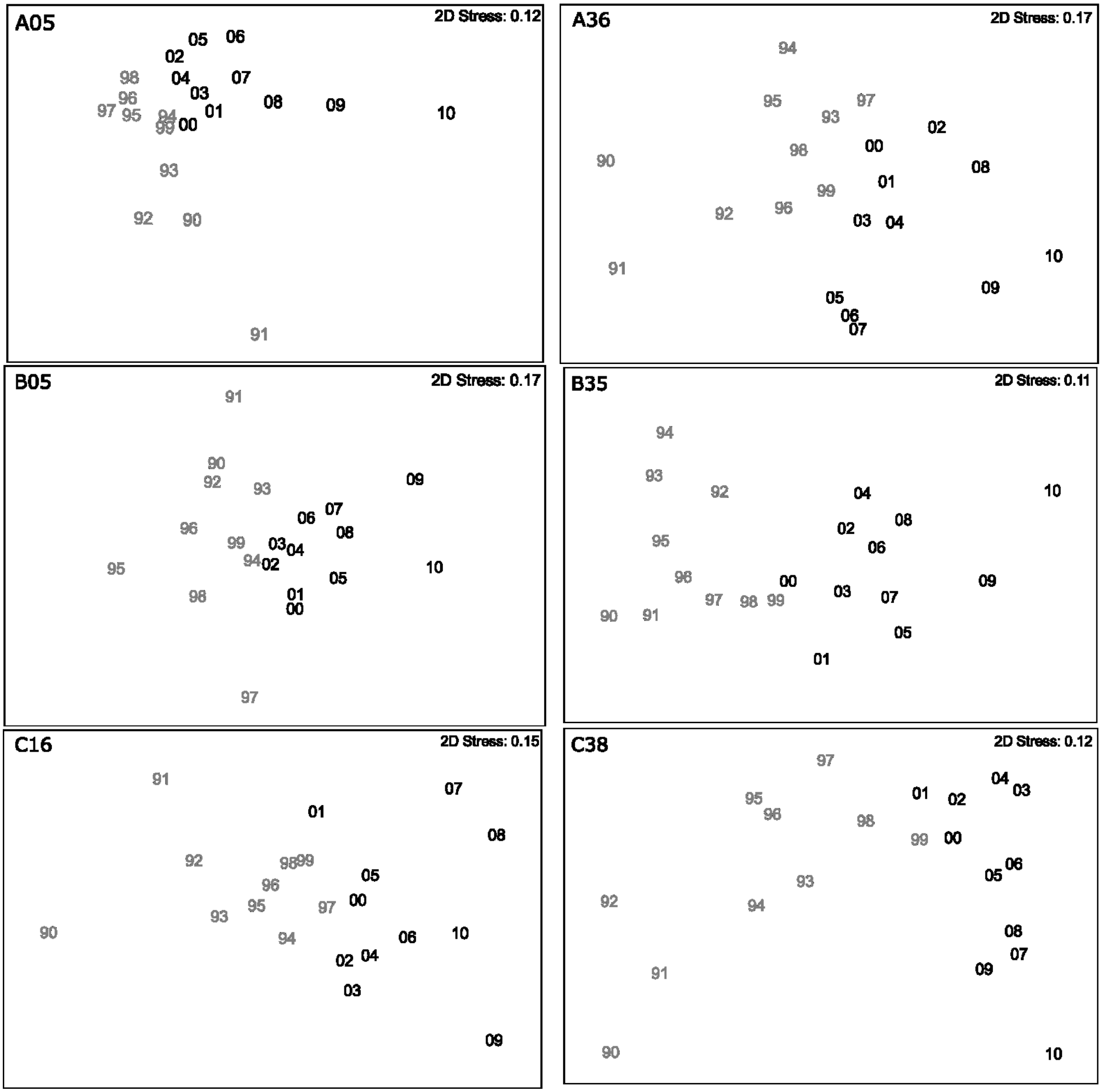


Figure 5. MDS-ordination (based on Bray-Curtis similarity) of soft bottom fauna from the six stations on the outer coast of South Norway from 1990-2010 (year 1990-1999 in grey, year 2000-2010 in black).

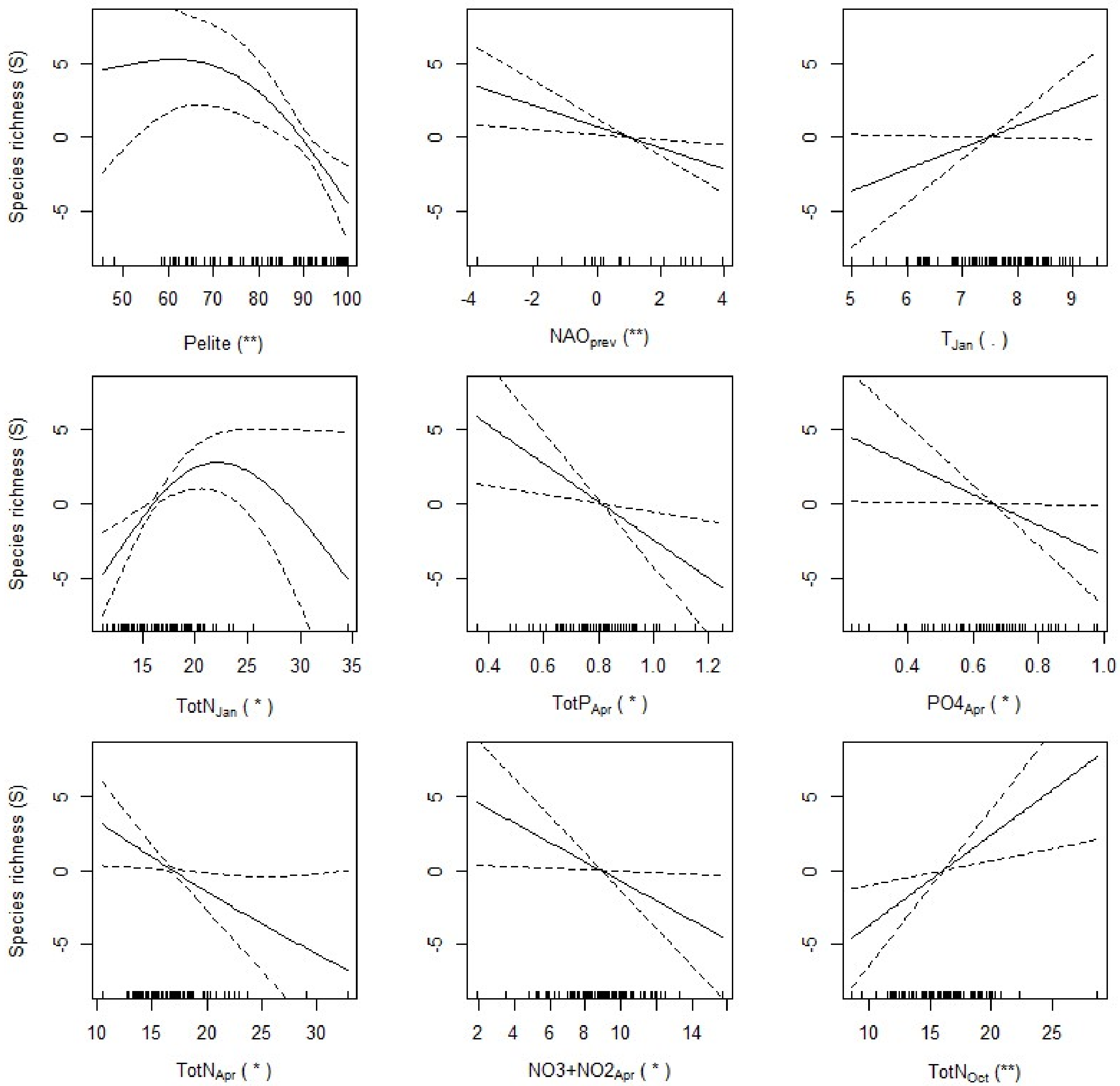


Figure 6. Predicted curves of species richness (S) based on univariable analyses of environmental variables used in the modelling (only relations with $p < 0.1$ are shown). Levels for *p* values are $p<0.01$ (**), $p<0.05$ (*), and $p<0.1$ (·). The y-axis is the effect on the response for each smooth and is centered around zero in order to ensure model identifiability for the smoothed responses.

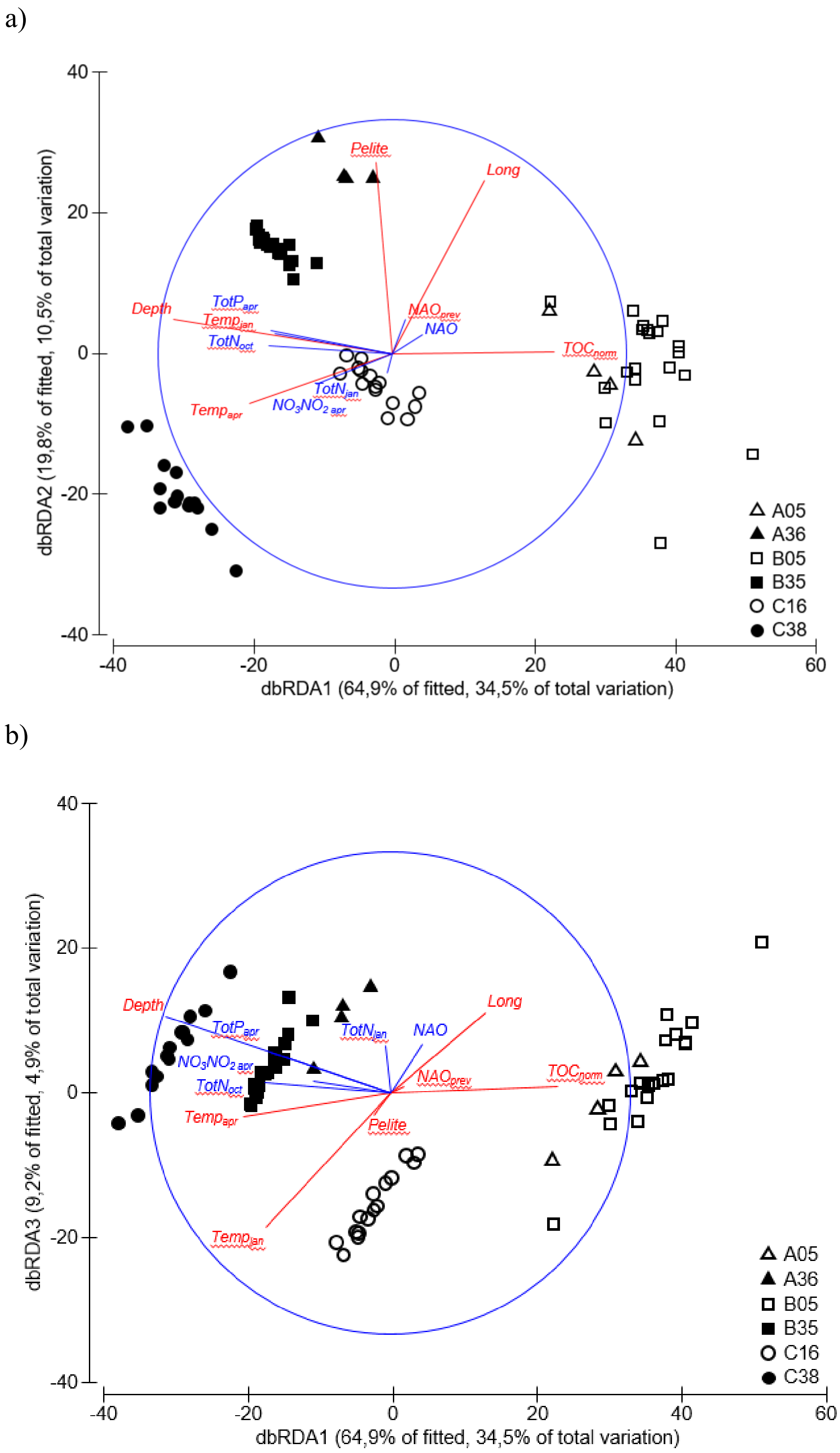
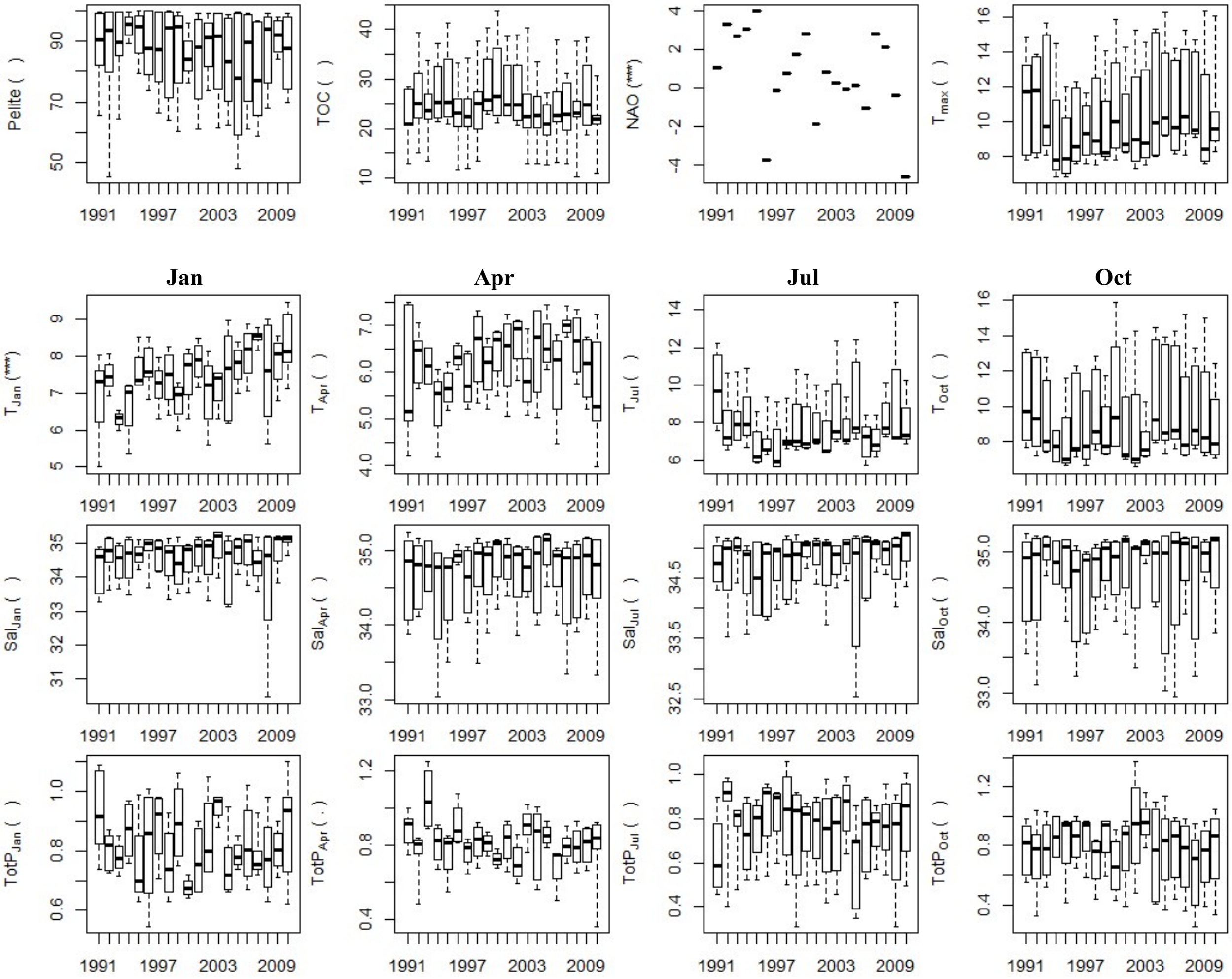


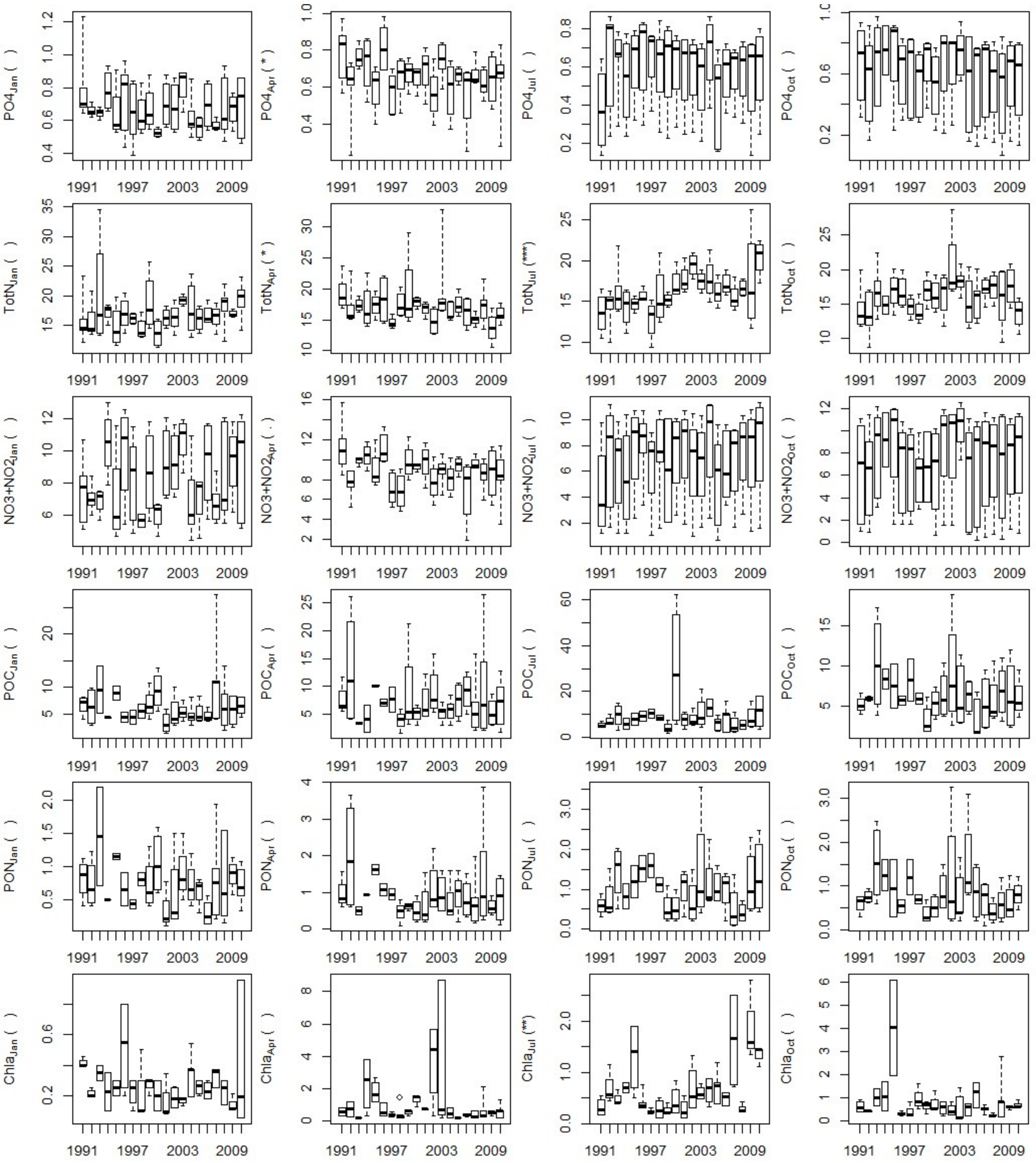
Figure 7. dbRDA plot of Bray Curtis similarity between samples based on soft bottom data for the period 1991-2010. Variables identified as significant by DistLM, are typed with red. a) axes 1 and 2, b) axes 1 and 3.

Supplement 1. Correlation matrix of all 48 environmental variables available. See main text for abbreviations.

	Lat	Long	Depth	Pelite	TOC	NAO	NAO$_{Prev}$	Temp$_{Max}$	Temp$_{Jan}$	Temp$_{Apr}$	Temp$_{Jul}$	Temp$_{Oct}$	SAL$_{Jan}$	SAL$_{Apr}$	SAL$_{Jul}$	SAL$_{Oct}$	TotP$_{Jan}$	TotP$_{Apr}$	TotP$_{Jul}$	TotP$_{Oct}$	PO$_4$P$_{Jan}$	PO$_4$P$_{Apr}$	PO$_4$P$_{Jul}$	PO$_4$P$_{Oct}$	TotN$_{Jan}$	TotN$_{Apr}$	TotN$_{Jul}$	TotN$_{Oct}$	NO$_3$NO$_{2Jan}$	NO$_3$NO$_{2Apr}$	NO$_3$NO$_{2Jul}$	NO$_3$NO$_{2Oct}$	POC$_{Jan}$	POC$_{Apr}$	POC$_{Jul}$	POC$_{Oct}$	PON$_{Jan}$	PON$_{Apr}$	PON$_{Jul}$	PON$_{Oct}$	POP$_{Jan}$	POP$_{Apr}$	POP$_{Jul}$	POP$_{Oct}$	Chla$_{Jan}$	Chla$_{Apr}$	Chla$_{Jul}$
Long	1.0																																														
Depth	0.0	-0.1																																													
Pelite	0.0	0.2	0.2																																												
TOC	-0.2	0.0	-0.7	0.3																																											
NAO	0.2	0.2	0.1	0.0	0.0																																										
NAO$_{Prev}$	0.2	0.2	0.0	0.1	0.0	0.0																																									
Temp$_{Max}$	0.4	0.4	-0.8	-0.2	0.6	0.0	0.1																																								
Temp$_{Jan}$	-0.4	-0.4	0.4	0.0	-0.3	-0.2	-0.3	-0.5																																							
Temp$_{Apr}$	-0.4	-0.5	0.6	-0.1	-0.5	0.1	-0.2	-0.6	0.5																																						
Temp$_{Jul}$	0.3	0.4	-0.7	-0.2	0.5	-0.1	0.2	0.8	-0.6	-0.7																																					
Temp$_{Oct}$	0.4	0.4	-0.8	-0.2	0.6	0.0	0.1	0.9	-0.5	-0.6	0.7																																				
SAL$_{Jan}$	-0.3	-0.4	0.8	0.1	-0.6	-0.1	-0.1	-0.8	0.7	0.6	-0.7	-0.8																																			
SAL$_{Apr}$	-0.3	-0.4	0.8	0.0	-0.6	-0.1	0.0	-0.8	0.5	0.8	-0.7	-0.7	0.8																																		
SAL$_{Jul}$	-0.3	-0.4	0.8	0.3	-0.5	0.0	0.0	-0.7	0.5	0.6	-0.8	-0.7	0.7	0.8																																	
SAL$_{Oct}$	-0.4	-0.4	0.8	0.3	-0.4	0.0	0.0	-0.8	0.5	0.6	-0.7	-0.8	0.8	0.7	0.9																																
TotP$_{Jan}$	0.2	0.1	0.5	0.1	-0.4	0.0	0.0	-0.3	-0.1	0.0	-0.1	-0.4	0.4	0.3	0.3	0.3																															
TotP$_{Apr}$	-0.1	-0.1	0.5	0.2	-0.3	-0.1	0.3	-0.4	-0.1	0.4	-0.3	-0.4	0.3	0.6	0.5	0.5	0.4																														
TotP$_{Jul}$	-0.2	-0.2	0.8	0.3	-0.5	0.1	0.0	-0.8	0.5	0.6	-0.8	-0.7	0.8	0.7	0.8	0.8	0.3	0.5																													
TotP$_{Oct}$	-0.3	-0.3	0.7	0.3	-0.5	-0.1	-0.1	-0.8	0.3	0.5	-0.6	-0.9	0.7	0.7	0.7	0.8	0.5	0.6	0.7																												
PO$_4$P$_{Jan}$	0.2	0.2	0.5	0.0	-0.4	0.0	0.3	-0.3	0.0	0.0	-0.2	-0.4	0.4	0.2	0.3	0.4	0.8	0.3	0.3	0.4																											
PO$_4$P$_{Apr}$	-0.2	-0.2	0.5	0.2	-0.4	0.0	0.3	-0.5	0.1	0.5	-0.4	-0.5	0.5	0.7	0.6	0.6	0.3	0.9	0.6	0.6	0.3																										
PO$_4$P$_{Jul}$	-0.3	-0.3	0.8	0.2	-0.6	0.1	0.0	-0.8	0.5	0.7	-0.9	-0.8	0.8	0.8	0.9	0.8	0.3	0.4	0.9	0.7	0.3	0.6																									
PO$_4$P$_{Oct}$	-0.2	-0.2	0.9	0.3	-0.6	0.0	0.0	-0.9	0.3	0.5	-0.7	-0.9	0.8	0.7	0.7	0.9	0.5	0.6	0.7	0.9	0.5	0.7	0.8																								
TotN$_{Jan}$	0.3	0.2	0.0	-0.1	-0.1	0.0	0.1	0.1	-0.3	-0.1	0.2	0.0	0.0	-0.1	0.0	0.0	0.3	0.1	-0.1	0.0	0.2	0.1	0.0	0.1																							
TotN$_{Apr}$	0.3	0.4	-0.1	0.1	0.1	0.1	0.4	0.2	-0.5	-0.2	0.3	0.2	-0.4	-0.2	-0.3	-0.3	0.2	0.3	-0.2	-0.1	0.0	0.2	-0.2	-0.1	0.2																						
TotN$_{Jul}$	-0.3	-0.2	0.3	0.1	-0.1	-0.3	-0.2	-0.3	0.2	0.3	-0.4	-0.3	0.3	0.4	0.3	0.3	0.2	0.1	0.4	0.4	0.1	0.2	0.3	0.3	0.0	-0.2																					
TotN$_{Oct}$	-0.4	-0.4	0.5	0.2	-0.2	0.0	-0.2	-0.5	0.3	0.5	-0.5	-0.5	0.5	0.5	0.5	0.6	0.3	0.4	0.4	0.7	0.3	0.4	0.5	0.6	0.0	-0.3	0.4																				
NO$_3$NO$_{2Jan}$	-0.1	-0.2	0.4	-0.1	-0.3	-0.1	0.1	-0.4	-0.1	0.1	-0.2	-0.4	0.4	0.2	0.2	0.3	0.6	0.3	0.2	0.4	0.6	0.3	0.3	0.4	0.3	0.1	0.2	0.4																			
NO$_3$NO$_{2Apr}$	-0.2	-0.2	0.3	0.0	-0.3	0.0	0.4	-0.3	-0.1	0.3	-0.1	-0.4	0.1	0.3	0.3	0.3	0.3	0.7	0.3	0.4	0.2	0.8	0.2	0.4	0.1	0.5	0.0	0.2	0.3																		
NO$_3$NO$_{2Jul}$	-0.4	-0.5	0.8	0.1	-0.6	0.0	0.0	-0.9	0.6	0.8	-0.9	-0.8	0.8	0.8	0.9	0.8	0.2	0.4	0.8	0.7	0.3	0.6	0.9	0.8	-0.1	-0.3	0.4	0.5	0.3	0.3																	
NO$_3$NO$_{2Oct}$	-0.4	-0.4	0.8	0.2	-0.6	0.0	-0.1	-0.9	0.4	0.6	-0.7	-1.0	0.8	0.8	0.8	0.9	0.4	0.5	0.7	0.9	0.4	0.6	0.8	1.0	0.0	-0.2	0.4	0.7	0.5	0.3	0.9																
POC$_{Jan}$	0.4	0.4	0.0	0.1	0.1	0.3	0.0	0.2	-0.1	-0.1	0.2	0.2	-0.3	-0.1	0.0	-0.2	0.0	-0.1	-0.1	-0.2	-0.2	-0.1	-0.1	-0.1	0.2	0.1	0.0	0.0	-0.4	-0.1	-0.2	-0.2															
POC$_{Apr}$	0.6	0.6	-0.1	0.0	0.1	0.1	0.0	0.4	-0.2	-0.3	0.2	0.4	-0.3	-0.3	-0.4	-0.5	-0.1	-0.3	-0.3	-0.3	-0.1	-0.5	-0.2	-0.3	0.0	0.2	-0.1	-0.3	-0.1	-0.4	-0.3	-0.4	0.3														
POC$_{Jul}$	-0.1	-0.1	-0.1	0.0	0.2	0.1	0.0	0.1	0.0	-0.1	0.1	0.2	-0.1	0.0	-0.1	-0.1	-0.3	-0.2	-0.1	-0.2	-0.3	-0.1	0.0	-0.2	-0.3	0.0	0.0	-0.2	-0.3	-0.1	0.0	-0.2	0.1	0.0													
POC$_{Oct}$	0.2	0.3	-0.4	0.1	0.5	0.0	-0.1	0.6	-0.4	-0.3	0.5	0.5	-0.5	-0.5	-0.5	-0.5	-0.2	-0.4	-0.4	-0.5	-0.2	-0.4	-0.5	-0.5	0.1	0.0	0.1	-0.1	-0.1	-0.4	-0.5	-0.5	0.2	0.4	0.1												
PON$_{Jan}$	0.4	0.5	-0.2	0.1	0.2	0.3	0.2	0.4	-0.4	-0.3	0.4	0.4	-0.5	-0.3	-0.3	-0.4	-0.1	-0.1	-0.3	-0.3	-0.2	-0.1	-0.3	-0.3	0.4	0.2	-0.1	-0.2	-0.3	-0.1	-0.4	-0.4	0.8	0.3	0.1	0.4											
PON$_{Apr}$	0.6	0.6	-0.2	0.1	0.1	0.1	0.0	0.4	-0.3	-0.4	0.3	0.4	-0.4	-0.4	-0.4	-0.5	-0.1	-0.3	-0.3	-0.4	-0.1	-0.5	-0.3	-0.4	0.0	0.3	-0.2	-0.4	-0.2	-0.4	-0.4	-0.4	0.3	1.0	-0.1	0.4	0.4										
PON$_{Jul}$	0.1	0.3	-0.6	0.1	0.6	-0.3	0.0	0.6	-0.3	-0.6	0.6	0.5	-0.5	-0.5	-0.6	-0.4	-0.2	-0.2	-0.5	-0.4	-0.3	-0.3	-0.6	-0.5	0.1	0.1	0.0	-0.3	-0.2	-0.3	-0.7	-0.5	0.1	0.2	0.2	0.6	0.3	0.3									
PON$_{Oct}$	0.2	0.3	-0.4	0.1	0.5	0.0	-0.1	0.6	-0.5	-0.4	0.5	0.5	-0.5	-0.6	-0.6	-0.5	-0.1	-0.3	-0.4	-0.4	-0.2	-0.4	-0.5	-0.5	0.1	0.1	0.1	-0.2	-0.1	-0.3	-0.6	-0.5	0.1	0.4	0.1	0.9	0.4	0.4	0.6								
POP$_{Jan}$	0.4	0.5	-0.2	0.1	0.2	0.3	0.2	0.4	-0.4	-0.3	0.4	0.4	-0.5	-0.3	-0.3	-0.4	-0.1	-0.1	-0.3	-0.3	-0.2	-0.1	-0.3	-0.3	0.4	0.2	-0.1	-0.2	-0.3	-0.1	-0.4	-0.4	0.8	0.3	0.1	0.4	1.0	0.4	0.3	0.4							
POP$_{Apr}$	0.6	0.6	-0.2	0.1	0.1	0.1	0.0	0.4	-0.3	-0.4	0.3	0.4	-0.4	-0.4	-0.4	-0.5	-0.1	-0.3	-0.3	-0.4	-0.1	-0.5	-0.3	-0.4	0.0	0.3	-0.2	-0.4	-0.2	-0.4	-0.4	-0.4	0.3	1.0	-0.1	0.4	0.4	1.0	0.3	0.4	0.4						
POP$_{Jul}$	0.1	0.3	-0.6	0.1	0.6	-0.3	0.0	0.6	-0.3	-0.6	0.6	0.5	-0.5	-0.5	-0.6	-0.4	-0.2	-0.2	-0.5	-0.4	-0.3	-0.3	-0.6	-0.5	0.1	0.1	0.0	-0.3	-0.2	-0.3	-0.7	-0.5	0.1	0.2	0.2	0.6	0.3	0.3	1.0	0.6	0.3	0.3					
POP$_{Oct}$	0.2	0.3	-0.4	0.1	0.5	0.0	-0.1	0.6	-0.5	-0.4	0.5	0.5	-0.5	-0.6	-0.6	-0.5	-0.1	-0.3	-0.4	-0.4	-0.2	-0.4	-0.5	-0.5	0.1	0.1	0.1	-0.2	-0.1	-0.3	-0.6	-0.5	0.1	0.4	0.1	0.9	0.4	0.4	0.6	1.0	0.4	0.4	0.6				
Chla$_{Jan}$	0.2	0.2	-0.2	0.1	0.1	-0.2	0.0	0.2	-0.3	-0.2	0.2	0.3	-0.3	-0.2	-0.1	-0.2	0.0	0.1	-0.1	-0.2	-0.2	0.0	-0.3	-0.2	0.2	0.1	0.0	-0.2	-0.4	0.1	-0.3	-0.3	0.2	-0.1	-0.2	0.1	0.3	0.0	0.1	0.2	0.3	0.0	0.1	0.2			
Chla$_{Apr}$	-0.2	-0.2	0.0	0.0	0.0	0.1	-0.2	-0.2	0.0	-0.1	-0.1	-0.2	0.1	-0.1	0.0	0.0	0.2	-0.1	0.0	0.2	0.2	-0.1	0.1	0.1	0.0	-0.2	0.1	0.3	0.3	-0.1	0.1	0.2	-0.1	0.1	0.0	0.1	-0.1	0.1	-0.2	0.0	-0.1	0.1	-0.2	0.0	-0.2		
Chla$_{Jul}$	-0.1	-0.1	0.0	0.1	0.1	0.0	-0.3	0.1	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.1	-0.1	-0.1	-0.1	-0.1	-0.3	-0.1	-0.1	-0.1	-0.1	-0.3	-0.1	0.0	-0.1	-0.2	0.0	-0.1	0.1	0.0	-0.1	0.2	0.0	0.0	0.1	0.2	0.0	0.0	0.1	0.2	0.1	-0.2	
Chla$_{Oct}$	0.1	0.2	0.1	0.2	0.1	0.2	0.3	-0.1	-0.2	-0.2	0.0	-0.1	-0.1	-0.1	0.0	0.0	-0.1	0.1	0.0	0.0	-0.1	0.0	0.0	0.1	0.0	0.2	0.0	-0.1	-0.1	0.0	0.0	0.0	0.2	0.2	-0.1	0.0	0.3	0.2	0.1	0.0	0.3	0.2	0.1	0.0	0.0	0.1	0.0

Supplement 2. Box (interquartile range) and whisker (extends to the most extreme data points) plots of yearly variation in measured environmental variables used in the soft bottom dataset, averaged for all stations. Symbols indicate significant levels at <0.001 (***), <0.01 (**), <0.05 (*), and <0.1 (·) for the regression through time for each environmental variable. Pelite content is measured as % particles < 0.063 mm, temperature (T) is given in °C, salinity (Sal) in ppt, Total Organic Carbon (TOC) in mg g^{-1} whereas all nutrients, i.e. total phosphor (TotP), phosphate (PO_4), total nitrogen (TotN), nitrate + nitrite (NO_3+NO_2), Particulate Organic Carbon (POC), and Nitrogen (PON) are given in μM.




PO4Jan ( )
PO4Apr (*)
PO4Jul ( )
PO4Oct ( )
TotNJan ( )
TotNApr (*)
TotNJul (***)
TotNOct ( )
NO3+NO2Jan ( )
NO3+NO2Apr (.)
NO3+NO2Jul ( )
NO3+NO2Oct ( )
POCJan ( )
POCApr ( )
POCJul ( )
POCOct ( )
PONJan ( )
PONApr ( )
PONJul ( )
PONOct ( )
ChlaJan ( )
ChlaApr ( )
ChlaJul (**)
ChlaOct ( )
1991
1997
2003
2009