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1 Soft bottom benthos and responses to climate variation and eutrophication in 2 Skagerrak

3
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8 9 10 **Abstract**

11 Skagerrak has been subject to several anthropogenic influences over the past decades, with
12 climate change and eutrophication being considered as the most serious and large-scale
13 disturbance factors. The present study reports monitoring data from six soft bottom stations in 50-
14 380 m depth at the Norwegian Skagerrak coast aimed at investigating to which degree changes in
15 environmental conditions have affected species communities and diversity. Sampling was carried
16 out yearly in the period 1990-2010. Links between benthic community patterns and climate
17 factors and physicochemical variables from the water masses were examined using uni- and
18 multivariate statistical methods. Throughout the period species richness gradually increased.
19 Although all stations showed distinct species assemblages, the community composition gradually
20 changed towards increased importance of sensitive small molluscs and tube-building annelids
21 concurrent with a general temperature increase and reduction of nutrients in the water masses.
22 The trend was largely similar over the stations, indicating that large-scale changes in the
23 Skagerrak water masses were driving factors compared to possible influences from local sources.
24 The faunal changes during the study period thus indicate an improved status of the soft bottom
25 benthos, which possibly could be related to a reduction in the eutrophication. On a shorter scale,
26 species richness was found to vary in relation to North Atlantic Oscillation (NAO) Index in the
27 previous year (decline), nutrient concentrations in spring (decline), and winter water temperature
28 (incline).

29
30 Keywords: Soft bottom benthos, species richness, climate change, eutrophication, time-series

31 32 33 **1. INTRODUCTION**

34
35 Climate change is both a global and a regional challenge. In the North Sea, water temperature has
36 increased 1-2 °C since 1985 (OSPAR 2010), and benthic communities have been documented to
37 be affected by temperature changes (e.g. Kröncke et al. 1998; Kröncke et al. 2011; Neumann &
38 Kröncke 2011). Climatic induced shifts in diversity patterns and species ranges have been
39 observed along the Norwegian coast (Narayanaswamy et al. 2010). Increasing temperature is
40 expected to increase the global rate of species extinction (Thomas et al. 2004), but in the coastal
41 zone indirect effects of climate change caused by e.g. increased runoff from land and increased
42 stratification may be more important on a short term. Frigstad et al. (2013) documented a regime
43 shift in seston and non-autotrophic material in coastal waters of the Norwegian Skagerrak early in
44 the 2000s, and suggested that effects of increased freshwater runoff, especially increased inputs
45 of terrestrial-derived, humic material, could play a role in the observed changes. At the same time
46 remarkable biological changes took place in the coastal waters, e.g. reduction in sugar kelp

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

55
56 Climate changes and eutrophication affect species composition of pelagic as well as benthic
57 ecosystems. Benthic communities are particularly suited for monitoring as the constituent species
58 are mainly sessile and integrate long-term effects of environmental change over time (Gray et al.
59 1990). As the species vary in sensitivity, the benthic communities undergo changes in
60 composition corresponding to the degree of disturbances (Pearson & Rosenberg 1978, Bilyard
61 1987, Olsgard & Gray 1995). In this regard, it is important to be aware that the long time-interval
62 over which degradation has occurred makes it difficult to determine the original status of the
63 ecosystem, and it is likely that many coastal areas have suffered from the 'shifting baseline
64 syndrome' (Pauly 1995, Dayton et al. 1998). Another challenging task in monitoring of benthic
65 communities is to understand and discriminate responses in cases of interacting effects where
66 community responses are likely to be complex and irregular. One attempt to understand
67 underlying patterns and disentangle natural variability and impacts from external factors, is
68 through the study of systematically sampled long-term data (e.g. Southward 1995, Hawkins et al.
69 2003). In the cases of anthropogenic eutrophication embedded within a climate signal, long-term
70 baseline data with extensive spatial and temporal coverage are strongly needed (Edwards et al.
71 2006).

72
73 Long-term monitoring of soft bottom communities in order to detect effects of external factors
74 has been carried out at several places in the North Sea. The longest time series is from two
75 stations (50 m and 80 m deep) at Northumberland (UK), which have been sampled since the
76 1970s. During the period there have been changes with approximately ten-year intervals in faunal
77 composition which could be related to climatic factors, production in overlying waters and
78 fishing intensity with various effects in different time periods (Frid et al. 2009a, b). Also in other
79 parts of the North Sea, time-series have documented long-term trends in the benthos, and that
80 faunal variation could be related to e.g. climatic factors, nutrient input, plankton as well as
81 freshwater-runoff (e.g. Tunberg & Nelson 1998, Hagberg & Tunberg 2000, Josefson & Hansen
82 2003, Reiss et al. 2006). Most studies have focused on patterns in species assemblages, but there
83 is currently an increasing interest in the use of biological traits, which can be defined as the
84 morphological, physiological, phenological or behavioral features of an organism that
85 describe its performance (Violle et al. 2014). Traits are often used as surrogates for ecosystem
86 properties as they have been documented to affect multiple ecosystem functions, and thus traits
87 analyses are increasingly used as means to improve the assessment of marine ecosystem
88 functioning including the understanding of the actual ecological significance of disturbance
89 effects (Oug et al. 2012, Beauchard et al. 2017).

90
91 In Norwegian waters, the Norwegian Coastal Monitoring Programme has monitored the
92 environmental status and development in coastal parts of Skagerrak since 1990 (Norderhaug et al.
93 2011). The programme has regularly collected data for soft bottom communities and shallow

94 subtidal hard bottom communities, as well as for climatic factors, nutrients, particle loading and
95 microalgae in the pelagic. Thus, the programme covers a multitude of environmental and
96 biological parameters from shallow to deeper areas in the Skagerrak and eastern North Sea. The
97 main aim of the programme has been to reveal possible effects of eutrophication and climate
98 change on the coastal ecosystems. It has been an important part of the project to distinguish
99 between the effects from long-distance transported substances and local sources.

100
101 Environmental management needs better information about complex ecosystem dynamics (Frid
102 et al. 2005), and about the single and interactive effects of disturbances such as eutrophication
103 and climatic variation on marine ecosystems. The aim of the present work is to examine the
104 development of the coastal soft bottom communities in the Skagerrak within the period 1990-
105 2010 and the influence of eutrophication and climatic variation. Specifically, spatial and temporal
106 changes in water temperature, salinity, nutrients, and suspended particles are related to species
107 richness, diversity, community structure and community functioning. The effects on shallow
108 water hard bottom systems for the same time period have been reported by Norderhaug et al.
109 (2015).

112 2. MATERIALS AND METHODS

114 2.1. Sea area characteristics

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

123
124 The Coastal Current and thereby Skagerrak receives large regional nutrient inputs from European
125 rivers (Aure & Magnusson 2008). The mean annual freshwater supply to the Skagerrak from the
126 Baltic Sea and the Kattegat is estimated to ca. $215\ 000\ \text{m}^3\ \text{s}^{-1}$, and in addition, a large fraction of
127 the $4\ 500\ \text{m}^3\ \text{s}^{-1}$ of continental river discharge to the North Sea passes through the area (Aure et
128 al. 1998). Particularly water from the German Bight strongly influences the water quality. This
129 water contributes to approximately 75% of nitrate and 40% of phosphate in the Coastal Current,
130 respectively, but in the period 1990-1995, when discharges from European rivers reached a
131 maximum level, the contribution was approximately 83% and 48%, respectively (Aure &
132 Magnusson 2008). Strong management effort has led to an improvement in the water quality,
133 although the current levels still are considerable higher than during earlier periods (1965-1980)
134 (Norderhaug et al. 2011). Notably, in contrast to declining nutrient concentrations, the
135 concentrations of carbon and nitrogen in seston, dissolved organic nitrogen and the estimated
136 fraction on non-autrophic material have been found to undergo a rapid increase between 1998
137 and 2000, and have remained at a higher level since (Frigstad et al. 2013). This increase is
138 probably caused by increased inputs of terrestrial-derived, humic material due to an increased
139 freshwater runoff (Frigstad et al. 2013).

140

141 **2.2. Sampling stations**

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

150

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

164

165 **2.3. Sampling and processing**

166 *2.3.1. Soft bottom fauna*

167 The six benthos stations were sampled with a 0.1 m² Day or van Veen grab in May or June each
168 year from 1990 to 2010, and fauna was sieved on a 1 mm screen. The field work and processing
169 were performed according to guidelines for quantitative sampling and sample processing of
170 marine soft-bottom macrofauna (NS-EN ISO 16665:2013). At each sampling occasion, either
171 four or eight grabs were sampled, but for the purpose of the present analyses four grabs (in the
172 case of eight, the first four) were used to make observations comparable. All specimens were
173 identified to species or lowest taxon possible. The species matrix of the faunal data consisted of
174 more than 140,000 individuals belonging to 531 taxa. Before analyses, abundances were
175 calculated as average values per 0.1 m² for each station and sampling occasion. The raw taxon
176 data matrix was inspected for inconsistencies in the identifications including changes in
177 taxonomy. Despite twenty years of data, very few persons have been involved in the
178 identification and care has been taken to transfer competence at change of personnel, which
179 reduces the chance of inconsistency in the species list.

180

181 *2.3.1. Environmental variables*

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

187 02:2013), the measured (*m*) TOC content was normalized (*n*) to adjust for varying sediment fine
188 fraction (*FF*):

$$189 \quad TOC_n(mg/g) = TOC_m(mg/g) + 18(1 - FF)$$

190
191 Temperature (T) and salinity (Sal) in the water masses were sampled monthly or bi-monthly at
192 the pelagic stations (Figure 1) with the use of CTD (i.e. Conductivity, Temperature and Depth
193 instrument). Simultaneously, water samples were taken and analysed for hydrochemical and
194 plankton contents that resulted in the following variables: total phosphorus (TotP), phosphate
195 (PO_4^{3-} , denoted PO_4), total nitrogen (TotN), nitrate + nitrite ($NO_3^- + NO_2^-$, denoted $NO_3 + NO_2$),
196 particulate organic carbon (POC) and nitrogen (PON) and chlorophyll a (Chla). The sampling
197 procedure was performed according to OSPAR Guidelines for the Joint Assessment and
198 Monitoring Programme (JAMP, OSPAR 2009) as well as ICES technical manuals and Guidance
199 on sampling from marine waters (NS-ISO 5667-9:1992).

201 **2.4. Data analyses**

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

212 *2.4.1. Environmental variables*

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

226
227
228 In addition to measured parameters, station depth, position (latitude and longitude) and the North
229 Atlantic Oscillation (NAO) index were entered among the environmental variables. NAO is a
230 measure of the strength of the sea-level air pressure gradient between Iceland and the Azores
231 (Bjerknes 1964). In the present study, the winter-based (December through February) NAO was
232 used. This variable was used in the analyses both for the same year as the biological sampling
233 (denoted NAO) and as a time-lagged variable, i.e. NAO for the previous year (denoted NAO_{prev}).

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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 were 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, PO₄, TotN, NO₃+NO₂).

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 m²) 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

281 cited by Magurran 1988), where S_{tot} is the total number of species collected per sampling
282 occasion, and S_{stn} is the average number of species per station (i.e. per 0.4 m²). The index
283 measures to which degree the whole investigated area is richer in species than the sampling
284 stations within the area.

285
286 All analyses of species richness and diversity at stations (S, H') with relation to the
287 environmental variables were carried out using R version 2.15.1 (R Development Core Team
288 2012). First, S, H' and all the 48 environmental variables available were tested for possible linear
289 time trends through the study period in univariable (i.e. individual) analyses using the `lm` function
290 in the R library `stats` (R Development Core Team 2012). Then, relationships between each
291 environmental factor and S and H' were assessed using the function `gamm` in the library `mgcv`
292 (Wood 2011) for Generalized Additive Mixed Models (Mixed GAM; Zuur et al. 2009). A
293 smoothing parameter (k) of max 3 was chosen for all continuous predictors, to allow for some
294 degree of non-linear effects, but not overfitting the models. Station ID was included as a random
295 factor in the GAMs to account for a potential dependence between observations taken at the same
296 site.

297
298 In subsequent analyses combinations of environmental variables for explaining species richness
299 (S) and diversity (H') were tested by model selection using mixed GAM. For this purpose, the
300 reduced dataset consisting of only the 15 preselected environmental variables were used. This
301 dataset consisted of variables that were only weakly correlated and had no missing data to meet
302 the criteria of model selection (Burnham et al. 2011). By the use of the R library `MuMIn` (Barton
303 2013), several thousand candidate models were tested, using all possible combinations of the 15
304 environmental predictor variables, and ranked by the use of Akaike Information criterion (AIC_c,
305 Burnham et al. 2011). Due to the limited number of degrees of freedom and the great number of
306 variables, interaction effects were not tested in the model selection procedure. Instead, the
307 potential non-additive effects of eutrophication and climate were analysed after finishing the
308 model selection by including their interaction to the best of candidate models that included the
309 two component variables of the interaction; each interaction in separate models.

310
311 Beta diversity was related to environmental variables by linear regression. All variables
312 representing climate and water mass characteristics (nutrients, particulate materials, chlophyll a)
313 were used. In order to maximise the number of variables, data from stn B05 were used and here
314 considered to reflect the major trends in the whole area (42 variables, omitting station position
315 and topography, see Table 2).

316
317 *2.4.4. Multivariate analyses - analysis of species composition and community functioning*
318 To analyse for similarities in the composition of species communities, non-metric
319 multidimensional scaling (nMDS) was used, based on Bray-Curtis similarity measure. Similarity-
320 calculations were based on fourth-root transformed data. This analysis was performed for the
321 complete biological dataset (i.e. all stations at all years; n = 126), in addition to each station
322 separately. Similarity percentage (SIMPER) analysis (Clarke 1993) was performed to obtain
323 information on changes in species composition during the time-period (1990-1999 vs. 2000-
324 2010). For analysing relationships between species composition and environmental variables,
325 Distance-based Linear Model (DistLM, Anderson 2001) was used. In order to obtain results that
326 could be comparable with the GAM-analyses, the same set of 15 environmental variables and
327 faunal data was used (see Table 2). Final inclusion of predictor variables in the model was based

328 on AIC_c criterium and a stepwise (which includes a forward as well as a backward step) selection
329 procedure. Sequential tests were done using 9999 permutations of residuals under the reduced
330 model. The ordination method of distance-based redundancy analysis (db-RDA) was used to
331 visualise the results. The db-RDA runs an eigen analysis and produces an ordination which is
332 constrained to be a linear combination of the environmental variables responsible for explaining
333 significant portions of the variation within the data cloud. DistLM and the corresponding db-
334 RDA were performed for the reduced data matrix. Also, marginal test was performed in DistLM
335 in order to quantify how much variation each variable explains alone, i.e. ignoring other
336 variables. The multivariate analyses were performed with PRIMER package version 6.1.13
337 (Clarke and Warwick, 2001).

338
339 To analyse for patterns in functional attributes of the species communities, biological trait
340 analysis (BTA) was conducted. Species abundance data were combined with traits data for each
341 species to calculate community weighted means (CWMs or ‘trait profiles’) expressing the
342 functional composition of the species assemblages (see Bremner et al. 2003, 2006, Oug et al.
343 2012, 2018, Beauchard et al. 2017). Nine traits representing adult life habit, degree of attachment,
344 mobility, size, body form, sediment dwelling depth, feeding mode, larvae type and sediment
345 reworking were used. These properties are key components of essential functions provided by
346 coastal benthic ecosystems, and are considered to reflect basic ecological aspects of the species,
347 including implications for sediment reworking and community stability. Each trait is divided in a
348 number of categories (2-9) that expresses different states of the trait. The species traits data were
349 extracted from a database held by Norwegian Institute for Water Research (NIVA) where
350 information has been compiled from a broad selection of literature and by consulting experts
351 (Oug et al. 2012), except for sediment reworking where data presented by Queirós et al. (2013)
352 on classification of soft bottom species with regard to bioturbation potential were applied.
353 Species traits were scored according to the ‘fuzzy coding’ procedure (Chevenet et al. 1994) with
354 values ranging from 0 (= no affinity) to 3 (= dominant) (see Oug et al. 2012, 2018 for further
355 details on trait categories and calculations). The analysis was carried out on a matrix of 187
356 species by omitting rare species (abundance < 0.0001% of total) and some few more of low
357 abundance lacking traits information. In the resulting matrix the traits information was complete
358 except for larvae type where data were missing for 15% of the species. The analysis was
359 performed with principal coordinate analysis PCoA (= metric MDS based on Euclidean distance
360 for calculation of similarities) in PRIMER package version 6.1.13. Prior to the analysis, species
361 data were fourth-root transformed as for the MDS. The ordination was based on the distances
362 among centroids for each station divided between 1990-1999 and 2000-2010.

363

364

365 **3. RESULTS**

366

367 **3.1. General faunal characteristics**

368 Altogether, 531 taxa and more than 140,000 individuals and were recorded in the samples. The
369 species assemblages were generally characterized by small annelids and mollusks. The deep
370 stations A36 in the outer Oslofjord and B35 along the southeast coast were very similar regarding
371 sediment characteristics and faunal composition. The mean sediment fine fraction was as high as
372 99% at both stations. The fauna was dominated by small bivalves (e.g. *Thyasira equalis* and *Abra*
373 *nitida*) and annelids (e.g. *Paramphinome jeffreysii*, *Heteromastus filiformis* and *Tharyx* sp.). The

374 deep station C38 at the southwest coast had coarser sediment, with a fine fraction of 76%. This
375 station was mainly dominated by annelids (e.g. *Myriochele heeri*, *Galathowenia oculata*), brittle
376 stars (e.g. *Amphilepis norvegica*) as well as the ostracode *Philomedes lilljeborgi*. The shallow
377 station A05 in the outer Oslofjord had a sediment fine fraction of 63%, and a fauna consisting
378 mainly of annelids (*H. filiformis*, *Chaetozone setosa* and *Prionospio fallax*), Nemertea and brittle
379 stars (e.g. *Amphiura chiajei*). The sediment was finer at B05 at the southeast coast, with a mean
380 fine fraction of 87%, despite its shallow location. Here, the fauna was dominated by annelids
381 (e.g. *Diplocirrus glaucus* and *C. setosa*), Nemertini, gastropods (e.g. *Hyala vitrea*) and bivalves
382 (e.g. *Ennucula tenuis*). Station C16 at intermediate depth at the southwest coast had a sediment
383 fine fraction as high as 90%, and annelids (e.g. *H. filiformis*, *Spiophanes kroyeri* and *P. jeffreysii*)
384 and small bivalves (*T. equalis* and *Kelliella miliaris*) dominated the fauna.

385
386 In the MDS-ordination of all stations (Figure 2), the samples were mainly clustered according to
387 station and depth, although C38 also seemed somewhat different from the others (A36, B35, and
388 C16). Station C16 showed the largest variation during the period. Notably, the samples from C16
389 in 2009 and A05 in 1991 and 2010 were separated from the main groups, but except from this all
390 stations more or less kept their identity throughout the monitoring period.

391
392 The analysis of community functioning revealed a main grouping based on station and depth,
393 roughly similar to the analysis of community structure (Figure 3). The horizontal axis largely
394 reflects a geographical gradient, whereas the vertical axis reflects depth with the deep stations at
395 the bottom of the plot. The functional features that contribute most to the ordination pattern were
396 represented by a variety of different traits (life habit, mobility, feeding habit, size, larvae type,
397 degree of attachment and sediment reworking) (Figure 3). The horizontal axis can be interpreted
398 as a gradient from high relative abundance of free-living burrowing and carnivorous species (left;
399 eastern stations) to a general dominance of non-mobile surface and deposit feeders (right; western
400 stations). Larvae type was highly correlated to the vertical axis, with increased dominance by
401 lecithotrophic larvae towards the deep stations and dominance by planktotrophic larvae towards
402 the shallow stations.

403

404 3.2. Temporal variation in faunal characteristics

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

411

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

421
422 Temporal changes were also seen in the analysis of community functioning (Figure 3). The
423 increase of shell-bearing molluscs and tube-building annelids and the decrease of free-living
424 annelids were reflected in the increase of attachment and permanent tubes and the decrease of
425 mobility, displayed on the first axis. The changes were most apparent at the deep stations (B35,
426 C38), where non-mobile surface and deep deposit feeders increased from the 1990s to the 2000s.
427 At the more shallow stations (A05, B05), suspension feeders with planktonic larvae appeared to
428 increase, whereas unattached subsurface deposit feeders decreased in the same period.
429

430
431 **3.3. Temporal variation in environmental variables**
432 During the monitoring period, the climate in Skagerrak and North Sea was generally mild, and
433 NAO indices were positive or close to zero during winter, with relatively high temperatures and
434 more than average precipitation in most years (Supplement 2). However, in 1996, 2010 and partly
435 2001, the winter weather was cold and dry, resulting in strongly negative NAO indices. January
436 temperatures increased steadily (linear regression: $p < 0.0001$) during the monitoring period, while
437 the other temperature variables did not show the same linear trend (Supplement 2). Regarding
438 nutrient concentrations, a trend with decreasing April concentrations was evident, which was
439 significant for PO_{4Apr} and $TotN_{Apr}$, and close to significant for NO_3+NO_{2Apr} and $TotP_{Apr}$. A
440 significant linear trend with increasing concentration throughout the time-period was found for
441 $TotN_{Jul}$, however, a sudden increase took place in the late 1990s, and a linear trend does not
442 describe the pattern well. A similar increase was recorded for Chl_{aJul} towards the end of 2000s. In
443 general, Chl_a had some extreme values in certain years, and general trends were not obvious
444 (Supplement 2).
445

446 **3.4. Environmental effects on species richness and diversity**
447 The response of species richness (S) and diversity (H') to all selected environmental variables
448 were first analysed in individual, univariable (i.e. one single environmental variable in each
449 model) Mixed GAMs, see Figure 6 (only relations with $p < 0.1$ are shown). Regarding diversity
450 (H'), no variables were significant, thus no plots are presented from these analyses. Species
451 richness responded significantly to the pelite content and NAO (for the previous year) and to
452 various variables related to the nutrient content of the water column ($TotN_{Jan}$, $TotP_{Apr}$, PO_{4Apr} ,
453 $TotN_{Apr}$, NO_3+NO_{2Apr} and $TotN_{Oct}$). There was weak evidence for increasing species richness
454 with increasing temperature in January ($p = 0.060$, Figure 6). In general, lower species richness
455 was found after a spring with high concentrations of nutrients, while the opposite was true for
456 autumn conditions the previous year as $TotN_{Oct}$ was associated with an increase in species
457 richness. A predominantly positive response was also observed for low and medium levels of
458 $TotN_{Jan}$, however a negative, but uncertain, effect was also found at high levels of $TotN$ (Figure
459 6).
460

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

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

473
474 For species richness, on the other hand, nine different candidate models were regarded as equally
475 good, since their $\Delta AICc$ were less than 2 (Burnham et al. 2011). These nine models included four
476 or five variables, represented by 11 of the 15 environmental variables tested. Only NO₃+NO_{2Apr},
477 T_{Apr}, TOC, and TotP_{Jan} were not included in any of these models. Further, when checking the
478 AICc-values for the interaction models, most of them were considerably better than their additive
479 counterpart.

480
481 To be able to compare the relative importance of the environmental variables against each other,
482 a set of the best models was examined. The models included most of the variables tested, but still
483 had sufficient support from the data. A $\Delta AICc$ level of <7 was thus chosen (Burnham et al.
484 2011), resulting in a set of 35 and 10 models of species richness and diversity, respectively
485 (Table 4). For species richness, the most important variable was depth, with a Relative
486 Importance Value (RIV, ranging from 0 to 1) of 0.996 (meaning it was included in almost all of
487 the 35 models considered). Depth was followed by the pelite content (RIV=0.69), NO₃+NO_{2Jan}
488 (RIV=0.59), TotP_{Apr} (RIV=0.36), T_{Jan} (RIV=0.34), TotN_{Oct} (RIV=0.18), NAO_{prev} (RIV=0.17),
489 and longitude (RIV=0.07). Although the importance values were far lower for diversity than for
490 species richness, it can be worth noting that TotN_{Oct} (RIV=0.11) and depth (RIV=0.07) were
491 ranked as the most important variables; the rest was only 0.04 or less. Model averaging (Burnham
492 and Anderson 2002) of the 35 best models of species richness and the 10 best models of diversity
493 (H') resulted in models explaining 56% ($R^2=0.56$) and 5% ($R^2=0.049$) of the variation of species
494 richness and diversity, respectively.

495
496 Due to the limited number of degrees of freedom, interactions were not included in the model
497 selection procedure. Instead, each possible variable combination of eutrophication and climate
498 was included as interactions to the best of the candidate models that included the two component
499 variables of the interaction. In the case of species richness, models with an interaction generally
500 performed better than models without, and in fact all of the 35 models with $\Delta AICc<7$ included an
501 interaction. Also for diversity, the interaction models ranked high (from rank 14 and further),
502 although no interaction models were among the 10 best models with $\Delta AICc<7$.

503
504 For beta diversity, there was a significant ($p < 0.05$) relationship for five variables related to
505 temperature, nutrients and chlorophyll in July the previous year (positive for T_{Jul_prev}, POC_{Jul_prev},
506 PON_{Jul_prev}, Chl_{aJul_prev}; negative for PO_{4PJul_prev}). NAO, temperature in January and salinity in
507 January (all positive) were close to significant ($p \leq 0.1$).

508 **3.5. Environmental effects on changes in fauna composition**

509
510 Faunal community composition responses to environmental variables were examined with
511 DistLM (Table 5). Of the 15 environmental variables examined, 7 were identified as significant
512 in the sequential test, and these variables collectively accounted for 55% of the variance in the
513 fauna. Depth, longitude, pelite, TOC, T_{Jan}, T_{Apr} and NAO_{prev} were identified as significant
514 variables for the community composition, while NO₃+NO_{2Apr} and TotN_{Jan} were close to

515 significant ($p < 0.077$). In the marginal test, where each variable is considered alone, 12 of the 15
516 variables were significant.

517
518 In the corresponding db-RDA plot (Figure 7 a and b), the samples were grouped according to
519 stations on the two first axes, as in the MDS-ordination. The first axis was mainly correlated to
520 depth, while the second axis mainly to sediment pelite content and longitude, thus these three
521 variables were the main descriptors for the variation between stations. The third axis was mainly
522 correlated to longitude, TOC, T_{Jan} and T_{Apr} . While depth and longitude are station-specific
523 variables, T_{Jan} and T_{Apr} vary through time. Altogether, the first three RDA-axes explained 86% of
524 the fitted variation, and 51% of the total variation of the multivariate community data. All of the
525 RDA-axes together explained 100% of the fitted variation and 60% of the total variation.

526
527

528 4. DISCUSSION

529

530 4.1. Patterns in community composition and functional traits

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

544

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

553

554 A significant increase in species richness was recorded through the monitoring period from 1990
555 to 2010, with especially low richness the two first monitoring years (1990 and 1991). A similar,
556 but not significant, positive trend was also observed for diversity. It may be noted that 1990 and
557 1991 were placed in the periphery in the ordination plots of several stations, indicating that these
558 years also were different from the following years regarding species composition. These findings
559 correspond well with patterns of species richness and total abundance in the western North Sea,
560 where Frid et al. (2009a, b) observed a change in the fauna around 1991, which they interpreted

561 as a benthic, lagged response of the “regime shift” in the North Sea plankton community. An
562 alternative, or supplementary explanation for the changes observed in Skagerrak, is that the
563 pattern might be related to a recovery phase after the bloom of the toxic algae *Prymnesium*
564 *polylepis* (syn. *Chrysochromulina polylepis*). In 1988 an extensive bloom of this toxic flagellate
565 occurred over much of the Skagerrak. Although the main concern of this alga was its effect on
566 littoral wild fish and farmed fish, also the soft bottom fauna was affected (Olsgard 1993). At an
567 impacted area in the western part of Skagerrak (ca. 34 km northwest of station C38), there was a
568 documented clear switch in species composition immediately following the bloom, and a
569 tendency of the fauna to return to the pre-bloom communities one to two years after the event
570 (Olsgard 1993). However, at the most severely affected stations examined by Olsgard, effects
571 appeared to still be present after three years (Gjøsæter et al. 2000).

572
573 The analysis of community functioning (Figure 3) revealed that e.g. “suspension feeding” was a
574 more important feature at the shallow stations than at the deeper stations. Presumably the shallow
575 stations are more exposed to bottom currents and suspended particles in the water, which the
576 suspension feeders may benefit on. Larvae type was also highly correlated to depth, with
577 increased occurrence of lecithotrophic larvae, i.e. larvae with short or no pelagic stage, towards
578 the deep stations and increase of planktotrophic larvae towards the shallow stations. This finding
579 may again relate to food availability; as planktonic larvae depend on feeding and growing in the
580 plankton, they obtain more nutrients in shallow than in deeper water (Thorson, 1950). In addition
581 to depth, there was a geographical gradient in the functional traits. Towards the outer part of
582 Skagerrak, there was a larger occurrence of surface and deep deposit feeders, also typically with
583 low mobility.

584
585 The small annelids *Heteromastus filiformis*, *Paramphinome jeffreysii* and *Tharyx* sp. showed
586 marked reductions in abundance from the 1990s to 2000s (Table 3). These taxa are often
587 recorded in high densities in organically or otherwise disturbed sediments (e.g. Pearson &
588 Rosenberg 1978, Borja et al 2000). On the other hand, the tube-building annelids *Myriochele*
589 *heeri* and *Galathowenia oculata* and the bivalve *Abra nitida* increased in abundance (Table 3).
590 Although these species may thrive in slightly organically enriched or physically disturbed
591 sediments, they are usually not present in highly disturbed environments (e.g. Holte & Gulliksen
592 1998, Borja et al 2000). Furthermore, shell-bearing molluscs and tube-building annelids were
593 among the increasing species, while free-living annelids and nemerteans were decreasing.
594 Generally, larger, tube-building species are more sensitive towards disturbances than free-living,
595 smaller species (e.g. Pearson & Rosenberg 1978, Oug et al. 2012). In total, the change in species
596 richness and species composition observed suggests an improvement of the soft bottom benthos
597 during the study period.

599 **4.2. Environmental variables and patterns in species assemblages**

600 The underlying mechanisms causing spatial gradients and changes with time in species
601 communities may include numerous environmental factors and biotic relationships (Gray & Elliot
602 2009). Several relationships are well described, whereas others are complex, and not well
603 understood. In the present study, a set of environmental variables was designated for four main
604 relationship groups; location and topography (depth, longitude), sediment conditions (pelite,
605 TOC), climate (temperature, NAO) and food supply (nutrient levels; assumed to reflect the
606 pelagic production). Variables for location and topography, and to some extent sediments, mostly
607 represent differences between the sampling stations, whereas variables for climate and nutrients

608 represent time-dependent environmental changes.

609
610 The analyses showed that environmental variables could be related both to species richness and
611 species composition. No relationships were detected for diversity (H'), however. The reason is
612 not clear, but the composite structure of H' , with one part based on species richness and the other
613 on equitability, may complicate the relationships. For instance, simultaneous changes in number
614 of species and individuals may not necessarily affect H' (Gray & Elliott, 2009).

615
616 Environmental variables from all four main relationship groups were significantly related to
617 faunal patterns. Variables representing basic station 'properties' such as depth, location and
618 sediment grain size (pelite) accounted for the larger fractions of variance in species composition
619 (DistLM-analysis) and ranked among the most important for species richness (mixed GAM).
620 Basically, the strength of these variables supports the intended design of the monitoring
621 programme to include sampling sites with different environmental conditions. Variables related
622 to climate and nutrient loading were less strongly, though significantly related to the faunal
623 patterns. This finding suggests that the faunal variation at the various stations could be associated
624 with measurable changes in environmental parameters.

625
626 *4.2.1. Topography and sediment conditions*
627 Depth and sediment characteristics are well-known descriptors for soft-bottom fauna (e.g.
628 Ellingsen 2002, Gray & Elliott 2009). Depth is, however, less important as a factor *per se*, but
629 rather represents several factors that vary with depth and determine the basic conditions for the
630 fauna, for instance bottom currents, temperature, supply of food and quality of organic material
631 (Oug 1998, Goginaa et al. 2010, McCallumc et al. 2010). It may vary to which degree these
632 factors are characterized among other environmental variables that are used in the analysis. In
633 both the variable selection in DistLM-analysis and the GAM modelling of species richness, depth
634 ranked at the top possibly because it summarises the effects of several important factors. Grain
635 size may also act as a surrogate variable as it reflects e.g. sedimentation regime, available organic
636 matter, oxygen penetration and sediment stability (e.g. Gray & Elliott 2009). Content of organic
637 carbon (TOC) was significant for species composition, but did not add much to explain variation
638 in species richness. TOC also lumps various conditions by consisting of material of different
639 origins, and in various stages of decomposition (Oug 1998). Longitude scored high in DistLM,
640 but not when it came to species richness. The importance of longitude may reflect changes in
641 faunal composition from inner to outer parts of Skagerrak. This could be a consequence of large-
642 scale topography-dependent factors that regulate species distributions, such as recruitment and
643 larval transport in major current systems.

644
645 *4.2.2. Trends in climate and nutrients*
646 Several climate and nutrient related variables were identified as significant for species richness
647 and species composition. For the study area as a whole, it seemed that variation in the total
648 species richness expressed by beta-diversity was related to temperature, particulate material and
649 chlorophyll a in the water masses the year previous to the sampling (July_{prev}). Possibly, this may
650 reflect that supply of larvae into Skagerrak and recruitment to the benthic communities increased
651 in years with relatively high temperatures and summer phytoplankton biomass. At station level,
652 the most distinct relationships were observed for winter and spring measurements of temperature
653 and nutrients, i.e. measurements taken 2-5 months before the faunal samples. In particular,
654 temperature in January (T_{Jan}) was the first of the climate and nutrient variables to be selected in

655 the DistLM analyses and ranked high in importance in the GAMM modelling. It may be a rather
656 complex matter, however, to indicate which relationships were the most influential, considering
657 that many variables were excluded from analysis because of missing data, and several variables
658 were omitted due to high inter-correlations. Regrettably, all variables from the month of July the
659 year before sampling had to be omitted from the analyses at stations. The results, however,
660 indicate that the conditions in the water masses in the previous summer, and during winter and
661 spring influences the development of the benthic species communities. It may be noted that the
662 climate variable NAO for the previous year (winter) also was found to be important. This
663 variable may catch a different and more delayed effect on the fauna than the monthly averaged
664 temperature and nutrients variables.

665
666 Generally, species richness increased with reduced nutrient concentrations in spring (PO_{4Apr} ,
667 $TotP_{Apr}$, NO_3+NO_{2Apr} and $TotN_{Apr}$). Direct cause and effect relationships are not possible to
668 assess from the present study with no information on organic fluxes to the bottom, but the
669 correlations may represent rather general faunal changes to variations in nutrient enrichment.
670 Nutrients in April showed a decreasing trend during the study period from rather high
671 concentrations in the 1990s to lower concentrations towards 2010. This decrease is in accordance
672 with the general trend in coastal waters in Skagerrak (e.g. Norderhaug et al. 2011, Frigstad et al.
673 2013) and other coastal regions of the North Sea (e.g. Carstensen et al. 2006, van Beusenkomp et
674 al. 2008, Voss et al. 2011). The reduced winter and spring concentrations have been interpreted
675 as documentation of a reduced current-transported input of nutrients to the Skagerrak from the
676 southern North Sea (Aure & Magnusson 2008, Vermaat et al. 2008). The decreasing
677 concentrations co-occurred with the faunal shift from small free-living and tolerant annelids to
678 higher dominance of more sensitive small molluscs and tube-building annelids. Thus, the faunal
679 changes could possibly be interpreted as a response to reduced eutrophication, particularly since
680 several of the declining species are generally stimulated by moderate enrichment (see e.g.
681 Pearson & Rosenberg 1978). This is further supported by the concurrent studies of pelagic
682 microalgae in the Norwegian Coastal monitoring programme showing a considerable shift after
683 2001, with lower biomass and an altered species composition from 2002 until today compared
684 with the period 1994-2001 (Trannum et al. 2012). Also for zooplankton large changes have been
685 observed, e.g. a substantial reduction in *Oithona* spp. and *Paracalanus/Pseudocalanus* spp.
686 (Johannessen et al. 2011). Changes in primary production and the pelagic food web structure may
687 certainly have consequences for the food transport to the bottom, but the processes and links in
688 the pelagic systems involved and the amount and quality of nutrient matters that in the end reach
689 the bottom is difficult to ascertain (see e.g. Josefson 1990, Josefson et al. 1993, Salen-Picard et
690 al. 2002, Josefson & Hansen 2003). Pelagic processes will also be influenced by other factors
691 such as weather conditions and climate, complicating the interpretation of faunal changes in
692 relation to nutrient levels.

693
694 In contrast to the other nutrients, total nitrogen ($TotN$) showed a particular season-dependent
695 relationship to species richness. Increasing levels in autumn ($TotN_{Oct}$) and decreasing levels in
696 spring ($TotN_{Apr}$) were both associated with increased species richness, whereas a bell-shaped
697 relationship was found for winter values ($TotN_{Jan}$). Also, $TotN_{Jan}$ was the only nutrient variable
698 which was not significant in the marginal test in DistLM, indicating that there was no clear
699 relationship between this variable alone and the species composition. It may be noted that
700 Norderhaug et al. (2015) found the same bell-shaped response for $TotN_{Jan}$ on species richness on
701 hard bottom. Although macroalgae are directly influenced by nutrients, there may be a consistent

702 pattern, although not necessarily a direct link, between nitrate in winter and species richness on
703 both hard- and soft bottom.

704
705 NAO is a descriptor of climate and correlates with broad variations in weather conditions in
706 northern Europe. Several studies from the North Sea and Skagerrak areas have demonstrated
707 relationships between NAO and benthic species communities (Tunberg & Nelson 1998, Hagberg
708 & Tunberg 2000, Rees et al. 2006, Narayanaswamy et al. 2010, Kröncke et al. 2011). It has been
709 found that single species as well as whole communities and functional groups are correlated to
710 changes in NAO (Hagberg et al. 2004). The factors underlying these responses are not fully
711 understood (Reid & Valdés 2011), but what is assumed, is that the influence of meteorological
712 drivers on marine systems is complex, and involves not only influence on temperature and sea
713 currents, but also mediation through plankton and benthic-pelagic coupling that typically produce
714 time-lagged responses (Frid et al. 2009b). In the present study, it is worth noting that NAO for
715 the previous year seemed to be much more important than NAO for the same year, which indeed
716 points to a time-lagged response. In particular, factors affecting timing, amount and quality of
717 organic matter which settles on the sea floor may seem to be important (e.g. Tunberg & Nelson
718 1998, Pearson & Mannvik 1998, Rabalais et al. 2009, Kröncke et al. 2011). With a high NAO
719 there is larger inflow of warm and nutrient-rich water from the southern North Sea (Hjøllo et al.
720 2009). Further, weather conditions have a profound influence on freshwater runoff and material
721 transported from land into the sea. In mild and wet winters (high NAO), when precipitation and
722 thereby runoff is high, much plant debris and eroded soil material are transported into the coastal
723 waters. In Swedish waters, a relationship between nutrient transport from land and benthic
724 abundance and biomass has been established, assuming a link through phytoplankton production
725 (Josefson 1990, Tunberg & Nelson 1998).

726
727 Interestingly, NAO was not only found to be associated with changes in species composition, but
728 also with species richness, where an increase in NAO (i.e. mild winters) was accompanied by a
729 small, but consistent, decline in species richness the following year. A similar relationship was
730 documented by Rees et al. (2006) for the western North Sea. Rees et al. (2006) suggested that the
731 density and variety of species may be lower in response to warmer winters characterized by
732 westerly airflows, which was a common feature of the weather patterns in the 1990s. Further, as
733 discussed above, if an increase in NAO leads to increased organic matter content in the water-
734 column, a subsequent response of the benthos may take place, albeit with different time lags at
735 different depths. It is worth mentioning that an increase in T_{Jan} was associated with an increase in
736 species richness. This finding may apparently be in contrast to the relationship between NAO and
737 S, but it is important to have in mind that it was NAO_{prev} (i.e. NAO one year before T_{Jan}) which
738 was significant for the patterns in community structure and species richness. Further, as discussed
739 above, NAO is assumed to act through complex and time-lagged rather than direct mechanisms
740 (see also review by Birchenough et al. 2015).

741 742 *4.2.3. General considerations*

743 Despite the effects of eutrophication in general have been reduced during the last two decades,
744 climate change may counteract some of this positive trend (McQuatters-Gollop et al. 2009,
745 Rabalais et al. 2009). Indeed, nutrient inputs from some Norwegian rivers and aquaculture have
746 increased recently (Skarbøvik et al. 2010). Further, there has been an increase in seston, dissolved
747 organic nitrogen (DON) and non-autotrophic materials (Frigstad et al. 2013) as well as a
748 darkening of coastal waters, partly due to such increased runoff (Aksnes et al. 2009). Thus, there

749 appears to have been a shift towards increasing importance of local discharge sources relative to
750 long-distance sources (Aure & Magnusson 2008, Norderhaug et al. 2015), which is of general
751 concern. The massive reduction of sugar kelp *Saccharina latissima* that took place in the late
752 1990s in shallow inshore waters, assumed to be a consequence of higher summer temperatures
753 and increased siltation from freshwater runoff (Moy & Christie 2012), may be an early effect on
754 benthic ecosystems. On outer coast however, hard bottom communities are far less affected
755 (Norderhaug et al. 2015). In deeper water, no large-scale ecosystem changes have been observed,
756 but, still, the present study documents that there were significant changes in the soft bottom fauna
757 from the 1990s to the 2000s. This significant, though less dramatic changes in soft bottom fauna
758 reported here, evidence a dampened response in deeper ecosystems. This agrees with the general
759 results from the long-term studies in western North Sea where the soft bottom species
760 communities appear to have undergone decadal shifts more or less coordinated with changes in
761 dominant driving forces (Frid et al. 2009b). Complex mechanisms linking pelagic production and
762 benthos, greater longevity of benthos compared to planktonic organisms, and recruitment
763 dynamics of benthic species may contribute to explain the observed lagged and dampened
764 responses to changes in the pelagic systems (Frid et al. 2009a, b).

765
766 Thus, it is evident that there have been modifications of all ecosystem compartments around the
767 year 2000. Frigstad et al. (2013) considered the concurrent changes in nutrients and particulate
768 matter, zooplankton, fish populations and sugar kelp in the coastal waters of Skagerrak as
769 evidence of a regime shift. Such shift also concurs well with an ecosystem shift in the North Sea,
770 evidenced by several studies both for plankton (e.g. Beaugrand 2014) and benthic communities
771 (e.g. Dippner et al. 2010, Kröncke and Reiss, 2010; Kröncke et al. 2013). As pointed out in these
772 studies, the major driver behind the biological regime shift is probably related to a climatic
773 regime shift. Such climatic change will both have direct and indirect effects (see review by
774 Birchenough et al. 2015), where increased runoff from land and terrestrial derived material is
775 hypothesised as one of the most important impact mechanisms for the coastal ecosystems.

776
777 A large proportion of the variance in the biological patterns was not explained by the
778 environmental data, which is not uncommon in observational studies. Marine benthic
779 communities are highly complex and respond to a wide range of ecologically structuring
780 processes acting on different scales (Kraufvelin et al. 2011, Buhl-Mortensen et al. 2012), and it is
781 impossible to measure all the relevant parameters involved in these processes. Also the
782 environmental variables, despite seasonal measures, may not have been collected at the right time
783 to capture important peaks in the time-series. In the present study, some of the unexplained
784 variation can probably be attributed to factors that have not been characterized in the present set
785 of environmental variables, e.g. the *Prymnesium polylepis* bloom in 1988 which may have
786 affected the benthic communities. Further, biological controlling factors, causing variances in e.g.
787 recruitment patterns, competition and trophic group amensalism may add to such unexplained
788 variation (Oug 1998). Even at the very local scale there may be patchiness related to topographic
789 and hydrographical differences at the seabed not accounted for (Gundersen et al. 2011), which
790 will appear as stochastic variation in the data. Lastly, there was a slight discrepancy in the
791 sampling design between the soft bottom and pelagic stations, i.e. the samples were taken close to
792 each other, but not at exactly the same location and depth.

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802 **References**

- 803 Aksnes DL, Dupont N, Staby A, Fiksen Ø, Kaartvedt S, Aure J (2009) Coastal water darkening and implications for
804 mesopelagic regime shifts in Norwegian fjords. *Mar Ecol Prog Ser* 387:39-49
- 805 Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32-46
- 806 Aure J, Danielssen D, Svendsen E (1998) The origin of Skagerrak coastal water off Arendal in relation to variations
807 in nutrient concentrations. *ICES J Mar Sci* 55:610–619
- 808 Aure J, Magnusson J (2008) Mindre tilførsel av næringsalter til Skagerrak (Eng: Decreased supply of nutrients to
809 the Skagerrak coast). In: *Kyst og Havbruk 2*. Institute of Marine Research, Bergen
- 810 Barton K (2013) MuMIn: Multi-model inference. R package version 1.9.5. [http://CRAN.R-](http://CRAN.R-project.org/package=MuMIn)
811 [project.org/package=MuMIn](http://CRAN.R-project.org/package=MuMIn)
- 812 Beauchard O, Verissimo H, Queirós AM, Herman PMJ (2017) The use of multiple biological traits in marine
813 community ecology and its potential in ecological indicator development. *Ecological Indicators* 76: 81-96.
- 814 Beaugrand G, Edwards M, Legendre L (2010) Changes in marine biodiversity: implications for ecosystem
815 functioning and carbon cycles. *PNAS* 107: 10120-10124
- 816 Beaugrand G, Harlay X, Edwards M (2014) Detecting plankton shifts in the North Sea: a new abrupt ecosystem shift
817 between 1996 and 2003. *Mar Ecol Progr Ser* 502:85–104
- 818 Bilyard GR (1987) The value of benthic infauna in marine pollution monitoring studies. *Mar Pollut Bull* 18: 581-585
- 819 Birchenough SNR, Reiss H, Degraer S, Mieszkowska, et al (2015) Climate Change and Marine Benthos: A Review
820 of Existing Research and Future Directions in the North Atlantic. *WIREs Clim Change* 6(2):203-223,
821 doi:10.1002/wcc.330
- 822 Bjerknes J (1964) Atlantic air-sea interaction. *Adv Geophys* 10: 1-82
- 823 Boesch DF, Hecky R, O'Melia C, Schindler D, Seitzinger S (2006) Eutrophication of Swedish Seas. Report 5509 to
824 Swedish Environmental Protection Agency
- 825 Borja A, Franco J, Péres V (2000) A Marine Biotic Index to Establish the Ecological Quality of Soft-Bottom
826 Benthos Within European Estuarine and Coastal Environments. *Mar Poll Bull* 40: 1100-1114.
- 827 Bremner J, Rogers SI, Frid CLJ (2003) Assessing functional diversity in marine benthic ecosystems: a comparison of
828 approaches. *Mar. Ecol. Prog. Ser.* 254, 11–25
- 829 Bremner J, Rogers SI, Frid CLJ (2006) Methods for describing ecological functioning of marine benthic assemblages
830 using biological traits analysis (BTA). *Ecol. Ind.* 6, 609-622
- 831 Buhl-Mortensen L, Buhl-Mortensen P, Dolan MFJ, Dannheim J, Bellec V, Holte B (2012) Habitat complexity and
832 bottom fauna composition at different scales on the continental shelf and slope of northern Norway. *Hydrobiol*
833 685: 191-219.
- 834 Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic
835 approach, 2nd edn. Springer, New York
- 836 Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral
837 ecology: some background, observations, and comparisons. *Behav Ecol Sociobiol* 65: 23–35
- 838 Carstensen J, Conley DJ, Andersen JH, Aertebjerg G (2006) Coastal eutrophication and trend reversal: A Danish
839 case study. *Limnol Oceanogr* 51: 398-408
- 840 Chevenet F, Doledec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data.
841 *Freshw. Biol.* 31: 295-309
- 842 Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- 843 Clarke KR, Warwick RM (2001) Change in marine communities. An approach to statistical analysis and
844 interpretation. Plymouth Marine Laboratory, Plymouth. 2nd ed.
- 845 Dayton PK, Tegner MJ, Edwards PB, Raiser KL (1998) Sliding baselines, ghosts and reduced expectations in kelp
846 forest communities. *Ecol Appl* 8: 309–322
- 847 Dippner JW, Junker K, Kröncke I (2010) Biological regime shifts and changes in predictability, *Geophys. Res. Lett.*,
848 37, L24701, doi:10.1029/2010GL045696.
- 849 Edwards M, Johns DG, Leterme SC, Svendsen E, Richardson AJ (2006). Regional climate change and harmful algal
850 blooms in the northeast Atlantic. *Limnol Oceanogr* 51: 820-829

851 Ellingsen KE (2002) Soft-sediment benthic biodiversity on the continental shelf in relation to environmental
852 variability. *Mar Ecol Prog Ser* 232:15-27

853 Frid CLJ, Paramor OAL, Scott CL (2005) Ecosystem-based fisheries management: progress in the NE Atlantic. *Mar*
854 *Policy* 29: 461-469

855 Frid CLJ, Garwood PR, Robinson LA (2009a) Observing change in a North Sea benthic system: A 33 year time
856 series. *J Mar Syst* 77: 227-236

857 Frid CLJ, Garwood PR, Robinson LA (2009b) The North Sea benthic system: a 36 year time-series. *J Mar Bio. Ass*
858 *UK* 89: 1:10

859 Frigstad H, Andersen T, Hessen DO, Jeansson, E, Skogen MD, Naustvoll LJ, Miles MW, Johannessen T, Bellerby R
860 (2013) Long-term trends in carbon, nutrients and stoichiometry in Norwegian coastal waters: Evidence of a
861 regime shift. *Prog Oceanogr* 111:113- 124

862 Gjørøster JK, Lekve K, Stenseth NC, Leinaas HP, Christie H, Dahl E, Danielssen DD, Edvardsen B, Olsgaard F, Oug
863 E, Paasche E (2000) A long-term perspective on the *Chrysochromulina* bloom on the Norwegian Skagerrak
864 coast 1988: a catastrophe or an innocent incident? *Mar Ecol Progr Ser* 207: 201-218

865 Goginaa M, Glockzina M, Zettler ML (2010) Distribution of benthic macrofaunal communities in the western Baltic
866 Sea with regard to near-bottom environmental parameters. 1. Causal analysis. *J Mar Syst* 79: 112-123

867 Gray JS, Elliott M (2009) *Ecology of Marine Sediments. From Science to Management*, Oxford Univ Press, Oxford.

868 Gray, JS, Clarke KR, Warwick RM, Hobbs G (1990). Detection of initial effects of pollution on marine benthos: an
869 example from the Ekofisk and Eldfisk oilfields, North Sea. *Mar Ecol Prog Ser* 66: 285-299

870 Gundersen H, Bekkby T, Norling K, Oug E, Rygg B, Walday M (2011) Nature Index of Norway - spatial predictive
871 modelling of soft sediment reference conditions along the Norwegian coast. *ICES CM* 2011/G:08

872 Hagberg J, Tunberg BG (2000) Studies on the Covariation between Physical factors and the Long-Term Variation of
873 the Marine Soft Bottom Macrofauna in Western Sweden. *Est Coast Shelf Sci* 50: 373-385

874 Hagberg J, Tunberg BG, Wiekling G, Kröncke I, Belgrano A (2004) Effects of climate on benthic communities. In:
875 Stenseth N, Ottersen G, Hurrell JW, Belgrano A (eds): *Marine ecosystems and climate variation. The North*
876 *Atlantic: a comparative perspective*. Oxford Univ Press, p 115-121

877 Hawkins SJ, Southwards AJ, Genner MJ (2003) Detection of environmental change in a marine ecosystem -
878 evidence from the western English Channel. *Sci Tot Env* 310: 245-256

879 Hjøllø SS, Skigen MD, Svendsen E (2009) Exploring currents and heat within the North Sea using a numerical
880 model. *J Mar Syst* 78: 180-192

881 Holte B, Gulliksen B (1998) Common macrofaunal dominant species in the sediments of some north Norwegian and
882 Svalbard glacial fjords. *Polar Biol* 19: 375-382

883 Johannessen T, Dahl E, Falkenhaug T, Naustvoll LJ (2011) Concurrent recruitment failure in gadoids and changes in
884 the plankton community along the Norwegian Skagerrak coast after 2002. *ICES J Mar Scidoi*:
885 10.1093/icesjms/fsr194

886 Josefson AB (1990) Increase in benthic biomass in the Skagerrak-Kattegat during the 1970s and 1980s - effects of
887 organic enrichment? *Mar Ecol Prog Ser* 66: 117-130

888 Josefson AB, Hansen J (2003) Soft bottom macrobenthos. In: Ærtebjerg G, Andersen JH, Schou Hansen O (eds):
889 *Nutrients and Eutrophication in Danish Marine Waters. A Challenge for Science and Management*. National
890 Environmental Research Institute, p 76-79

891 Josefson AB, Jensen JN, Ærtebjerg G (1993) The benthos community structure anomaly in the late 1970s and early
892 1980s - a result of a major food pulse? *J Exp Mar Biol Ecol* 172: 31-45

893 Kraufvelin P, Persus J, Bonsdorff E (2011) Scale-dependent distribution of soft-bottom infauna and possible
894 structuring forces in low diversity systems. *Mar Ecol Prog Ser* 426: 13-28

895 Kröncke I, Dippner JW, Heyen H, Zeiss B (1998) Long-term changes in macrofaunal communities off Norderney
896 (East Frisia, Germany) in relation to climate variability. *Mar Ecol Prog Ser* 167: 25-36

897 Kröncke I, Reiss H (2010) Long-term variability of benthic indices off the island of Norderney in the southern North
898 Sea. *Marine Pollution Bulletin* 60: 58-68

899 Kröncke I, Reiss H, Eggleton JD, Aldridge J, Bergman MJN, et al. (2011) Changes in North Sea macrofauna
900 communities and species distribution between 1986 and 2000. *Estuar Coast Shelf Sci* 94: 1-15

901 Magurran AE (1988) *Ecological Diversity and its Measurement*. Chapman and Hall, London

902 McCallumc AW, Mellind C, Cresswelle ID, Radke LC (2010) On the use of abiotic surrogates to describe marine
903 benthic biodiversity. *Estuar Coast Mar Sci* 88: 21-32

904 McQuatters-Gollop A, Gilbert AJ, Mee LD, Vermaat JE, Artioli Y, Humborg C, Wulff F (2009) How well do
905 ecosystem indicators communicate the effects of anthropogenic eutrophication? *Estuar Coast Mar Sci* 82: 583-
906 596

907 Moy F, Christie H (2012) Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the
908 south and west coast of Norway. *Mar Biol Res* 8: 309-321

909 Narayanaswamy BE, Renaud PE, Duineveld GCA, Berge J, Lavaleye MSS, et al. (2010) Biodiversity Trends along
910 the Western European Margin. *PLoS ONE* 5(12): e14295. doi:10.1371/journal.pone.0014295.

911 Neumann H & Kröncke I (2011) The effect of temperature variability on ecological functioning of epifauna in
912 the German Bight. *Mar. Ecol.* 32: 1-9

913 NIVA (2002) Statlig program for overvåking: Kystovervåkingsprogrammet. Langtidsovervåking av miljøkvaliteten i
914 kystområdene av Norge. 10-årsrapport 1990-1999. NIVA Report 4543-2002. In Norwegian

915 Norderhaug KM, Ledang AB, Trannum HC, Bjerkeng B, Aure J, Falkenhaus T, Folkestad A, Johnsen T, Lømsland
916 E, Omli L, Rygg B, Sørensen K (201). Long-term monitoring of environmental quality in the coastal regions of
917 Norway. Klif-report TA-2777. ISBN 978-82-577-5869-1

918 Norderhaug KM, Gundersen H, Pedersen A, Moy F, Pedersen A, Green N, Walday MG, Gitmark, JK, Ledang, AB,
919 Bjerkeng, B, Hjermand, DØ, Trannum, HC (2015) Effects of climate and eutrophication on the diversity of
920 hard bottom communities on the Skagerrak coast 1990-2010. *Mar Ecol Prog Ser* 530:29-46.
921 <https://doi.org/10.3354/meps11306>

922 NS-ISO 5667-9:1992 Water quality - Sampling - Part 9: Guidance on sampling from marine waters

923 NS-EN ISO 16665:2013 Water quality – guidelines for quantitative sampling and sample processing of marine soft
924 bottom macrofauna

925 Olsgard F (1993) Do toxic algal blooms affect subtidal soft-bottom communities? *Mar Ecol Prog Ser* 102:279-286.

926 Olsgard F, Gray JS (1995) A comprehensive analysis of the effects of offshore oil and gas exploration and
927 production on the benthic communities of the Norwegian continental field. *Mar Ecol Prog Ser* 122: 277-306

928 OSPAR (2009) Monitoring and assessment series 447. OSPAR Commission, London

929 OSPAR (2010) Quality Status Report 2010. OSPAR Commission London.

930 Oug E (1998) Relating species patterns and environmental variables by canonical ordination: an analysis of soft-
931 bottom macrofauna in the region of Tromsø, northern Norway. *Mar Environ Res* 45: 29-45

932 Oug E, Fleddum A, Rygg B, Olsgard F (2012) Biological traits analyses in the study of pollution gradients and
933 ecological functioning of marine soft bottom species assemblages in a fjord ecosystem. *J Exp Mar Biol Ecol*
934 432-433: 94-105

935 Oug E, Sundet JH, Cochrane SKJ (2018) Structural and functional changes of soft-bottom ecosystems in northern
936 fjords invaded by the red king crab (*Paralithodes camtschaticus*). *J Mar Systems* 180: 255-264

937 Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol Evol.* 10: 430 (doi:10.1016/
938 S0169-5347(00)89171-5)

939 Pearson TH, Mannvik HP (1998) Long-term changes in the diversity and faunal structure of benthic communities in
940 the northern North Sea: natural variability or induced instability? *Hydrobiol* 375-376: 317-329

941 Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the
942 marine environment. *Oceanogr Mar Biol Ann Rev* 16 :229–311

943 Queirós AM, Birchenough SNR, Bremner J, Godbold JA, Parker RE, Romero-Ramirez A, Reiss H, Solan M,
944 Somerfield PJ, Colen CV, Hoey GV, Widdicombe S (2013). A bioturbation classification of European marine
945 infaunal invertebrates. *Ecol. Evolution* 3, 3958-3985

946 R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical
947 Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org/>

948 Rabalais NN, Turner RE, Díaz RJ, Justić D (2009) Global change and eutrophication of coastal waters. *ICES J Mar*
949 *Sci* 66: 1528-1537

950 Ramsay TO, Burnett RT, Krewski D (2003) The effect of concavity in Generalized Additive Models linking
951 mortality to ambient particulate matter. *Epidemiology* 14: 18-23

952 Rees HL, Pendle MA, Limpenny DS, Mason CE, Boyd SE, Birchenough S, Vivian CMG (2006) Benthic responses
953 to organic enrichment and climatic events in the western North Sea. *J Mar Biol Assoc UK* 86: 1-18

954 Reid PC, Valdés L (2011) ICES status report on climate change in the North Atlantic. ICES Cooperative Research
955 Report No. 310

956 Reiss H., Meybohm K, Kröncke I (2006) Cold winter effects on benthic macrofauna communities in near- and
957 offshore regions of the North Sea. *Helgol Mar Res* 60: 224-238

958 Salen-Picard C, Darnaude A, Arlhac D, Harmelin-Vivien M (2002) Fluctuations of macrobenthic populations: a link
959 between climate-driven river run-off and sole fishery yields in the Gulf of Lions. *Oecologia* 133: 380-388

960 Shannon CE & Weaver W (1963) The mathematical theory of communication. University of 663 Illinois Press,
961 Urbana

- 962 Skarbøvik E, Stålnacke P, Kaste Ø, Selvik J, Tjomsland T, Høgåsen T, Aakerøy T, Paul A, Beldring S (2010)
963 Riverine inputs and direct discharges to Norwegian coastal waters - 2009. KLIF report TA-2726
964 Southward AJ (1995) The importance of long time-series in understanding the variability of natural systems. *Helgol.*
965 *Meeresunters* 49: 329-333
966 Thomas CD, Cameron A, Green RE, Bakkenes M and others (2004) Extinction risk from climate change. *Nature*
967 427:145–8
968 Thorson G. (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25, 1–45.
969 Trannum (2012) Kystovervåkingsprogrammet. Skagerrak overvåket gjennom en tjue-års periode. No. 2905 2012. 4
970 pp. In Norwegian.
971 Tunberg BG, Nelson WG (1998) Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic
972 communities on the Swedish west coast? *Mar Ecol Prog Ser* 170: 85-94
973 Van Beusekom JEE, Weigelt-Krenz S, Martens P (2008) Long-term variability of winter nitrate concentrations in the
974 Northern Wadden Sea driven by freshwater discharge decreasing riverine loads and denitrification. *Helgol*
975 *Mar Res* 62: 49-57
976 Vermaat JE, McQuatters-Gollop A, Eleveld MA, Gilbert AJ (2008) Past, present and future nutrient loads of the
977 North Sea: Causes and consequences. *Estuar Coast Mar Sci* 80: 53-59
978 Violle C, Reich, PB, Pacala SW, Enquist BJ, Kattge J (2014) The emergence and promise of functional
979 biogeography. *Proceedings of the National Academy of Sciences USA* 111:13690–13696.
980 Voss M, Dippner JW, Humborg C, Hurdler J, Korth F, Neumann T, Schernewksi G, Venohr M (2011). History and
981 scenarios of future development of Baltic Sea eutrophication. *Est Coast Shelf Sci* 92: 307-322
982 Water Directive Guide 02:2013. Veileder 02:2013. Klassifisering av miljøtilstand i vann - Økologisk og kjemisk
983 klassifiseringssystem for kystvann, grunnvann, innsjøer og elver. (Eng: Classification of environmental status
984 in water – Ecological and chemical classification system for coastal water, groundwater, lakes and rivers).
985 Direktoratgruppen for gjennomføring av vandirektivet.
986 Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric
987 generalized linear models. *J Roy Stat Soc B* 73: 3–36
988 Zuur AF, Latuhihin MJ, Ieno EN, Baretta-Bekker JG, Smith GM, Walker NJ (2009) *Mixed Effects Models and*
989 *Extensions in Ecology with R.* Springer, New York
990

991 Table 1. Concurvity matrix of the 15 environmental variables included in the model selection using GAM and
 992 ordination analyses. Concurvity is the non-parametric analogue of collinearity (Ramsay et al. 2003), and can be
 993 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

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 995

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

Stations	Years																					
	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
A36	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
SE coast																						
	B05	38	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48	48
B35	14	15	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
SW coast																						
	C16	20	30	36	34	31	38	40	40	40	46	48	48	48	47	48	48	48	48	48	48	48
C38	14	15	15	14	14	15	15	15	13	15	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
C38	14	15	15	14	14	15	15	15	13	15	15	15	15	15	15	15	15	15	15	15	15	15

999
1000

1001 Table 3. SIMPER-analysis for all stations treated together for the time-categories 1990-1999 vs. 2000-2010, where
 1002 taxa representing 70% of the difference between the groups are included. Abundance (no. ind/0.1 m²), trend (“+”
 1003 denotes increase; “-“denotes decrease), average dissimilarity (AvDis. %) and cumulative average dissimilarity of
 1004 differences between the groups area also presented.

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

1005
1006

1007 Table 4. Importance table from the Mixed GAM analyses and model selection of species richness (S) and diversity
 1008 (H'). Variables are ranked according to their relative importance value (RIV) based on all models with $\Delta AIC_c < 7$.
 1009 RIV ranges between 0 and 1 and increases with its presence in the models considered, which was 35 and 10 for S and
 1010 H', respectively.

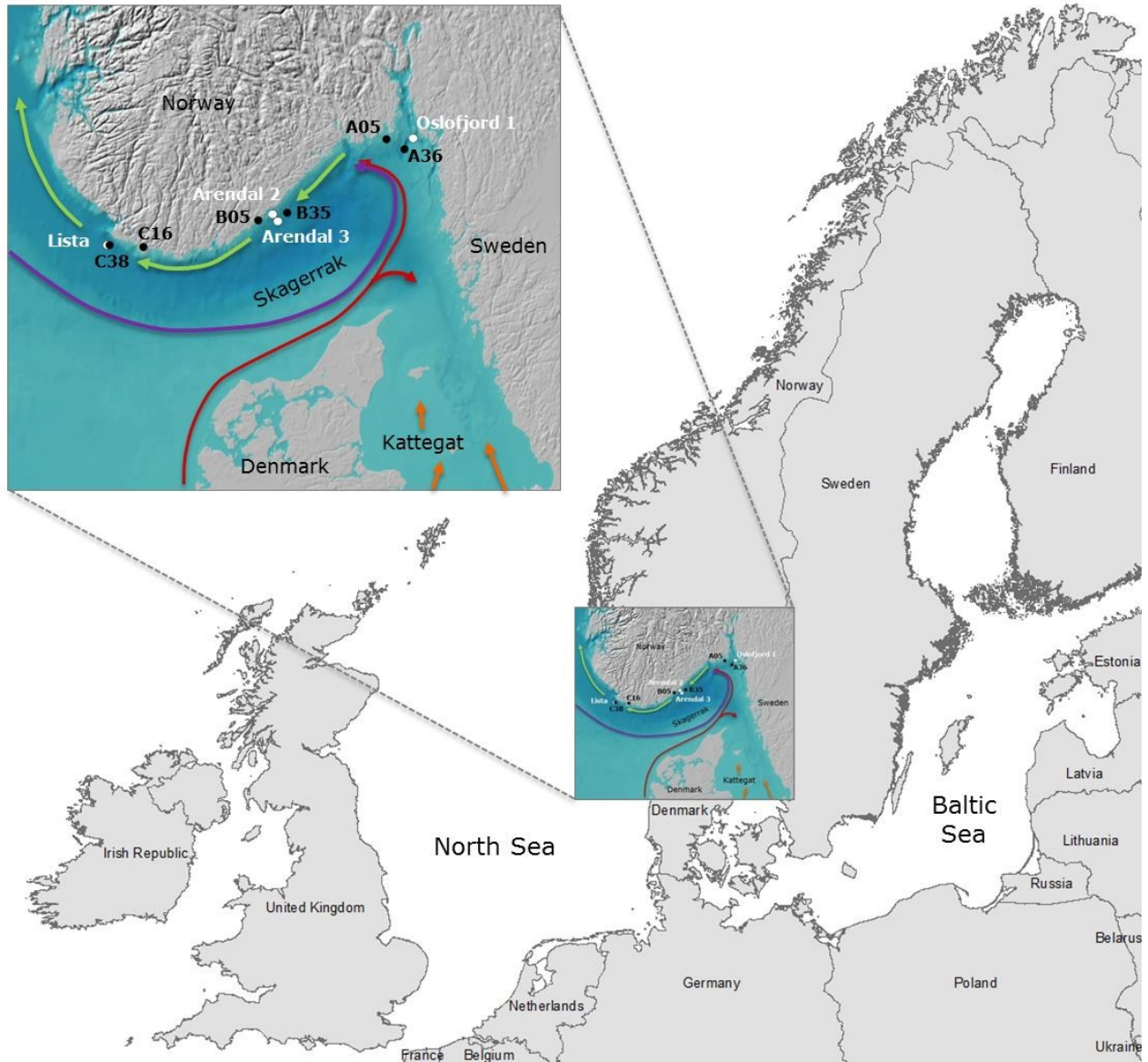
Variables	RIV (S)	Variables	RIV (H')
Depth	1.00	TotN _{Oct}	0.11
Pelite	0.69	Depth	0.07
NO ₃ +NO ₂ Jan	0.59	TotP _{Apr}	0.04
TotP _{Apr}	0.36	Pelite	0.04
T _{Jan}	0.34	Longitude	0.03
TotN _{Oct}	0.18	TotN _{Jan}	0.03
NAO _{prev}	0.17	NAO _{prev}	0.03
Longitude	0.07	NO ₃ +NO ₂ Jan	0.03
NAO	0.05	TotN _{Apr}	0.02
TotN _{Jan}	0.03	NAO	0.00
NO ₃ +NO ₂ Apr	0.00	NO ₃ +NO ₂ Apr	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

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1013 Table 5. Results of the DistLM-model, including Sum of squares (SS), Pseudo-F statistic, p-value and proportional
 1014 and cumulative explained total variance. Significant ($p < 0.05$) variables are in bold. Sequential tests explain the
 1015 cumulative variation attributed to each variable fitted to the model in the order specified, taking previous variables
 1016 into account. Marginal tests show how much variation each variable explains when considered alone, ignoring other
 1017 variables.

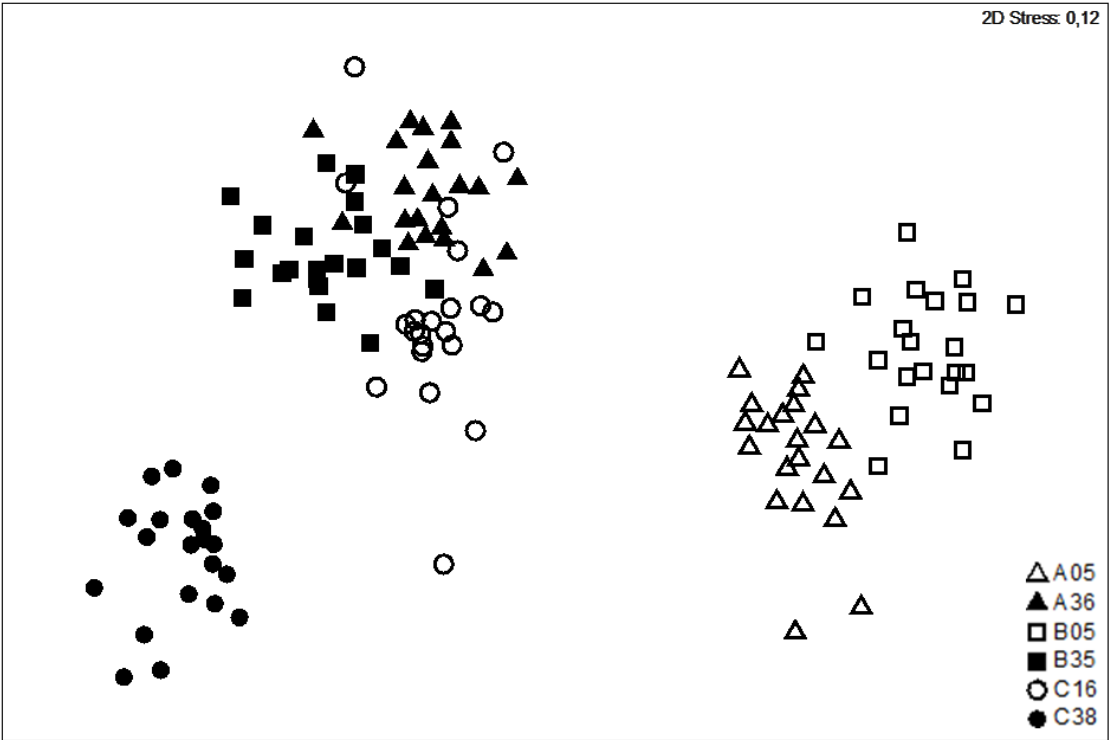
<i>Sequential test</i>	SS	Pseudo-F	p	Prop.	Cumul.
Depth	44874	33.59	<0.001	0.309	0.31
Longitude	13910	11.93	<0.001	0.096	0.41
Pelite	7147	6.59	<0.001	0.049	0.45
TOC	7643	7.69	<0.001	0.053	0.51
T_{Jan}	3544	3.70	<0.001	0.024	0.53
T_{Apr}	1901	2.01	0.006	0.013	0.55
NAO_{prev}	1427	1.53	0.049	0.010	0.56
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
<i>Marginal test</i>	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	
NO₃+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	
NO₃+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	

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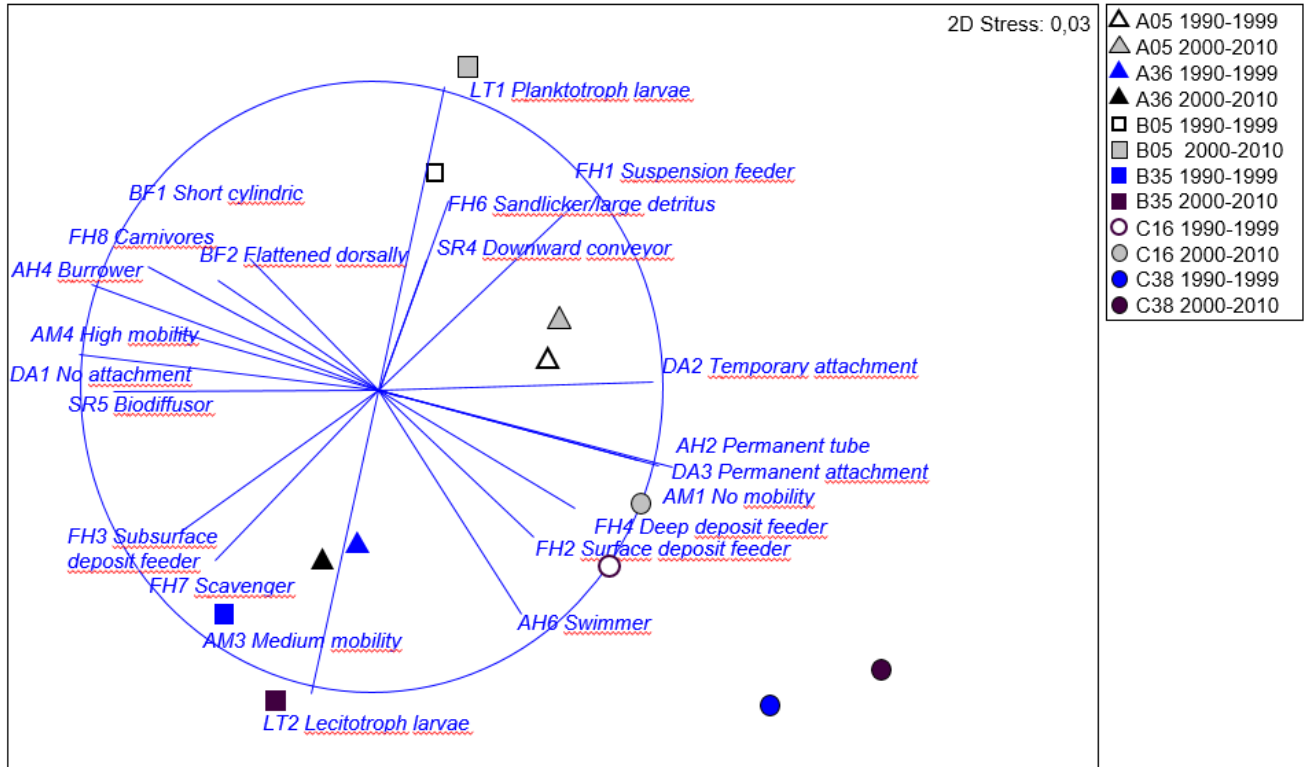
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Figure 1. Soft bottom (black dots) and pelagic (hydrophysical and hydrochemical, white dots) stations within the Norwegian Coastal Monitoring Programme. The stations were positioned in three regions: the outer Oslofjord (A), the southeast coast (B), 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.

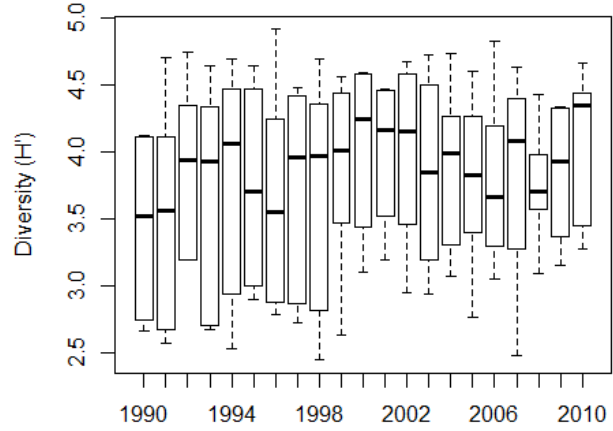
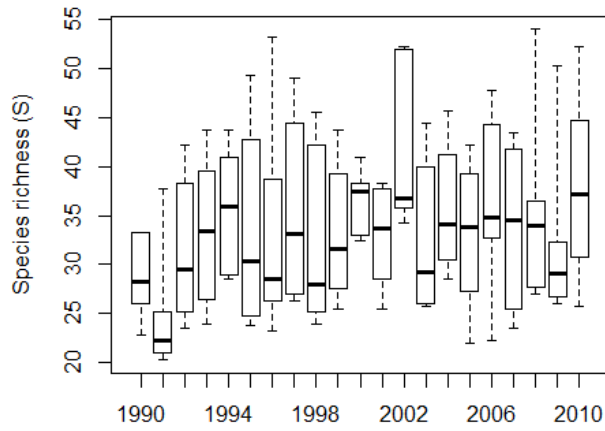


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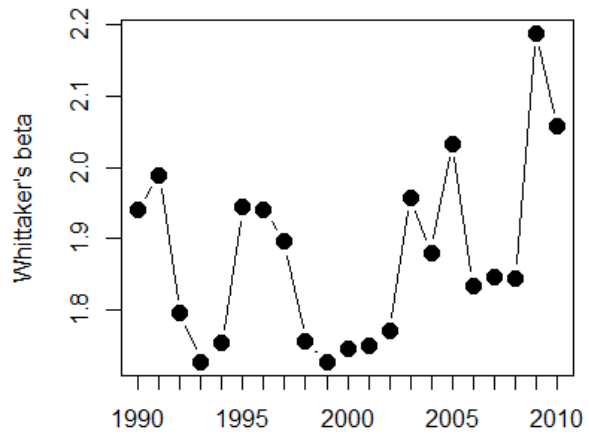
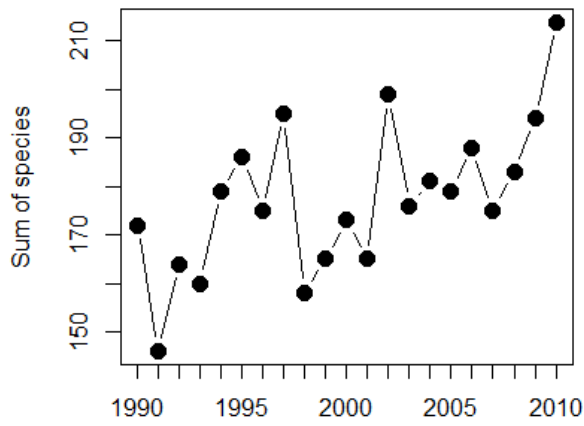
Figure 2. MDS-ordination (based on Bray-Curtis similarity) of soft bottom fauna on the outer coast of South Norway from 1990 to 2010.



1029
 1030 Figure 3. Principal coordinate analysis (PCoA) of species traits of soft bottom fauna on the outer coast of South
 1031 Norway from 1990 to 2010: biplot of station centroids (divided between 1990-1999 and 2000-2010 to indicate
 1032 temporal patterns) and trait categories. Trait categories are illustrated as vectors pointing in the direction of
 1033 maximum increase, long vectors indicate strong trends. For clarity, only traits with high correlation to the axes
 1034 (Pearson correlation coefficient > 0.6) are shown. These are adult life habit (AH), adult mobility (AM), body form
 1035 (BF), feeding habit (FH), larvae type (LT), degree of attachment (DA), sediment dwelling depth (SD) and sediment
 1036 reworking (SR).
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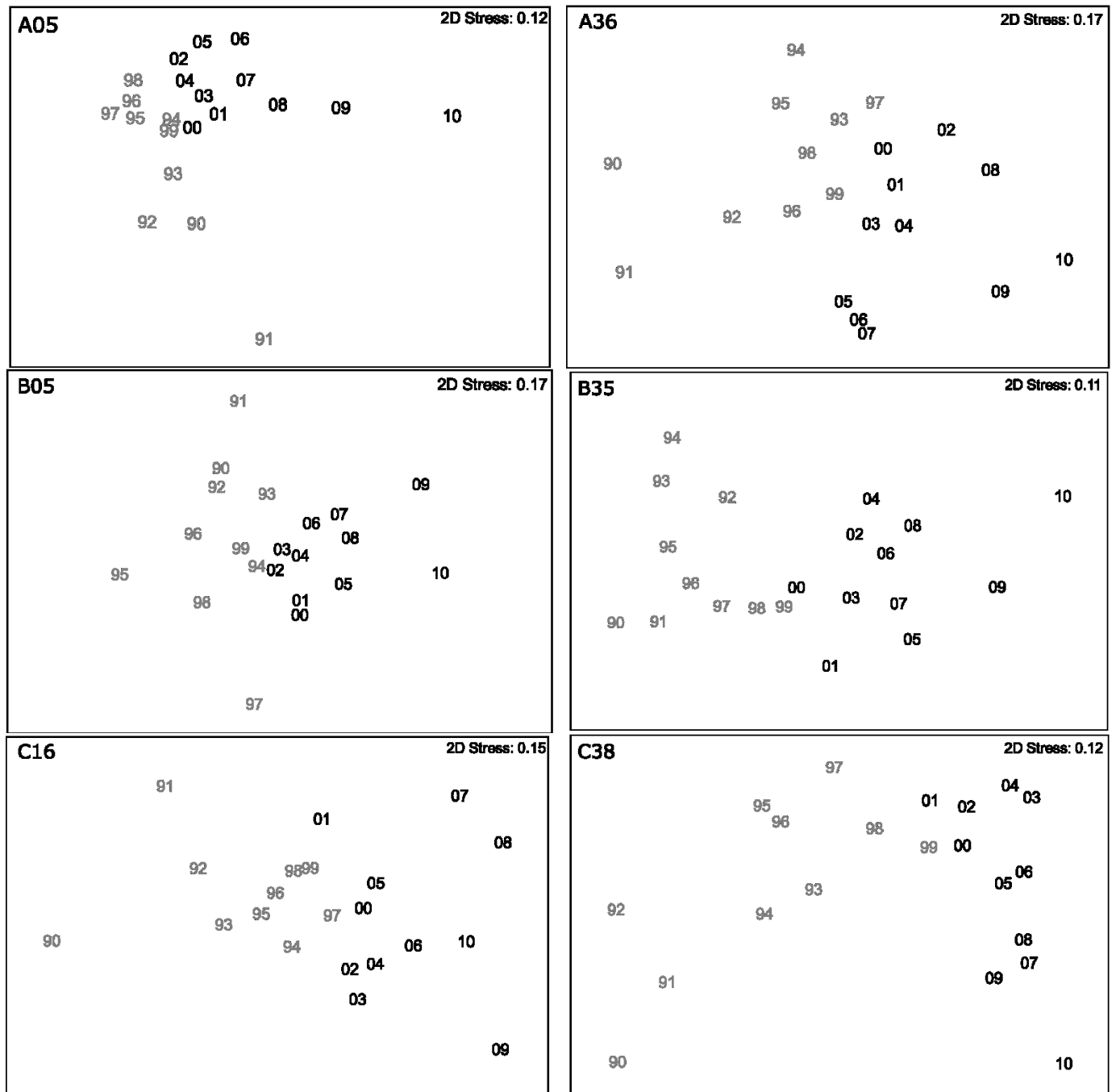


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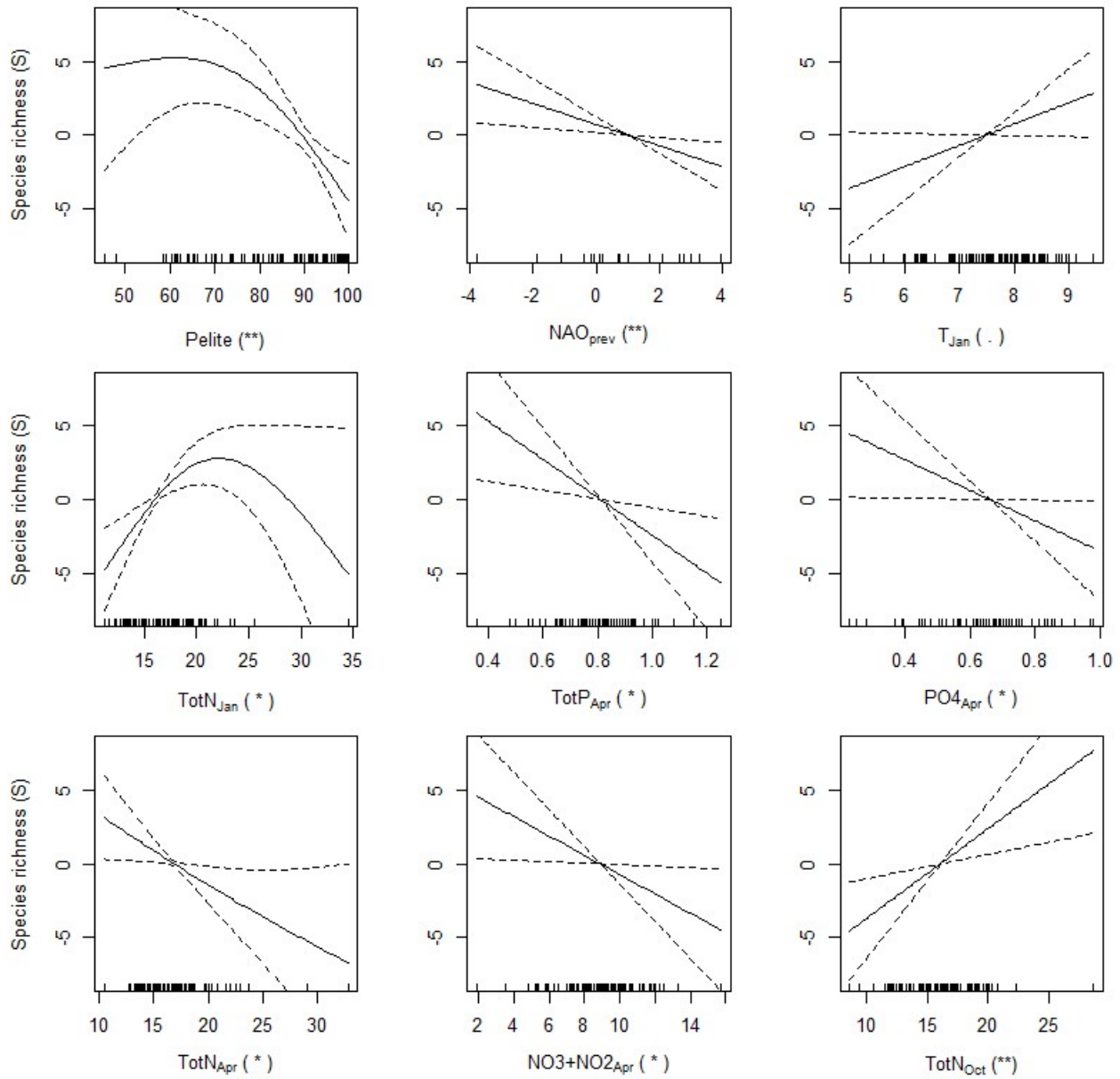


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Figure 4. Species richness and diversity of soft bottom fauna on the outer coast of South Norway 1990-2010. Top: Box (interquartile range) and whisker (extends to the most extreme data points) plots of species richness (S) and diversity (Shannon-Wiener 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.

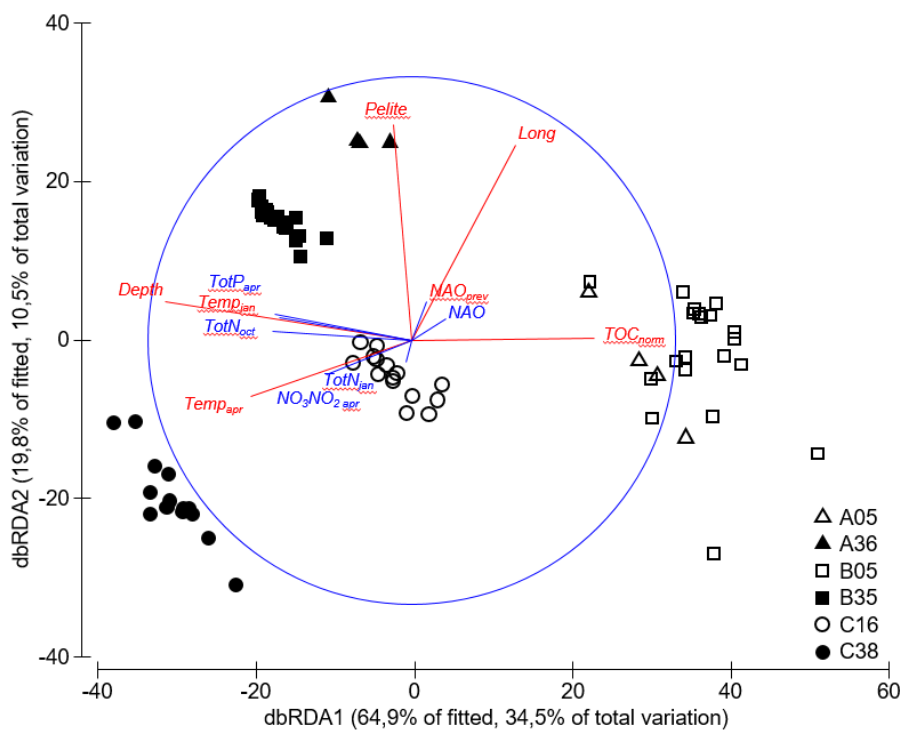


1046 Figure 5. MDS-ordination (based on Bray-Curtis similarity) of soft bottom fauna from the six stations on the outer
 1047 coast of South Norway from 1990-2010 (year 1990-1999 in grey, year 2000-2010 in black).
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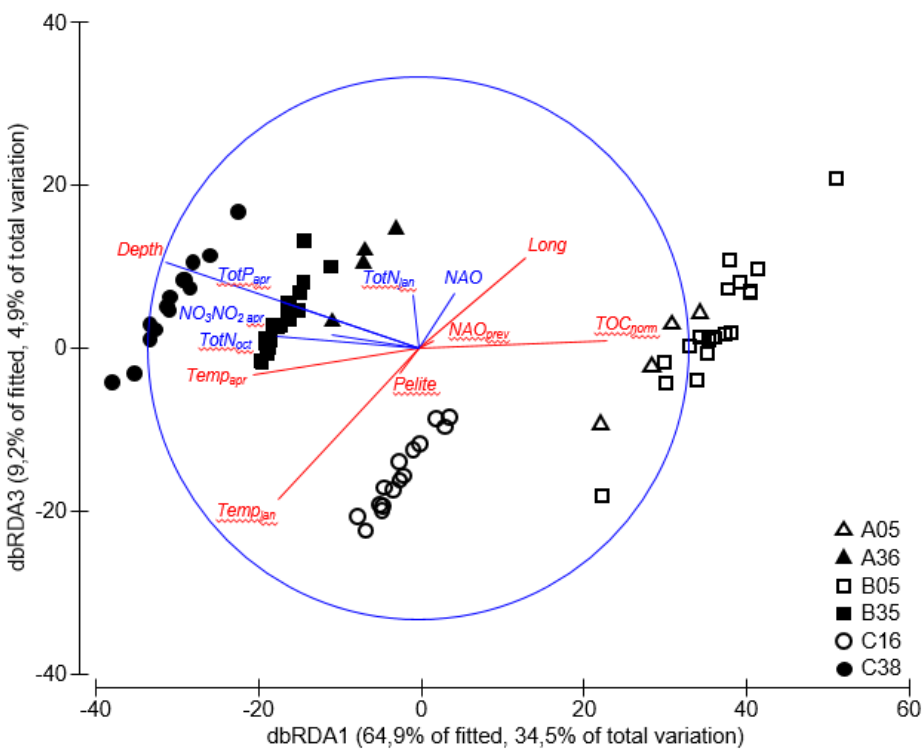


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 1050 Figure 6. Predicted curves of species richness (S) based on univariable analyses of environmental variables used in
 1051 the modelling (only relations with $p < 0.1$ are shown). Levels for p values are $p < 0.01$ (**), $p < 0.05$ (*), and $p < 0.1$ (·).
 1052 The y-axis is the effect on the response for each smooth and is centered around zero in order to ensure model
 1053 identifiability for the smoothed responses.
 1054

1055 a)



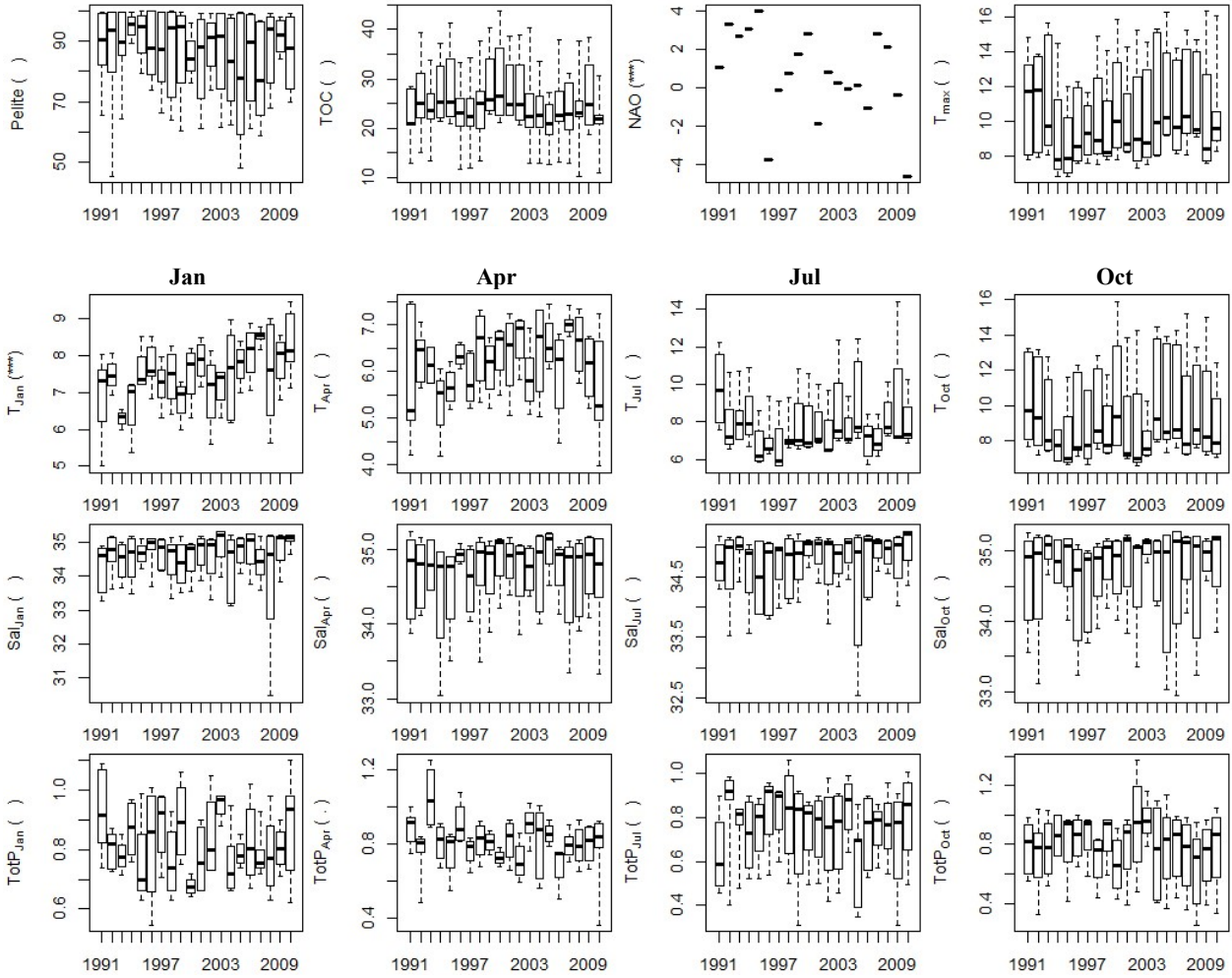
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1057 b)



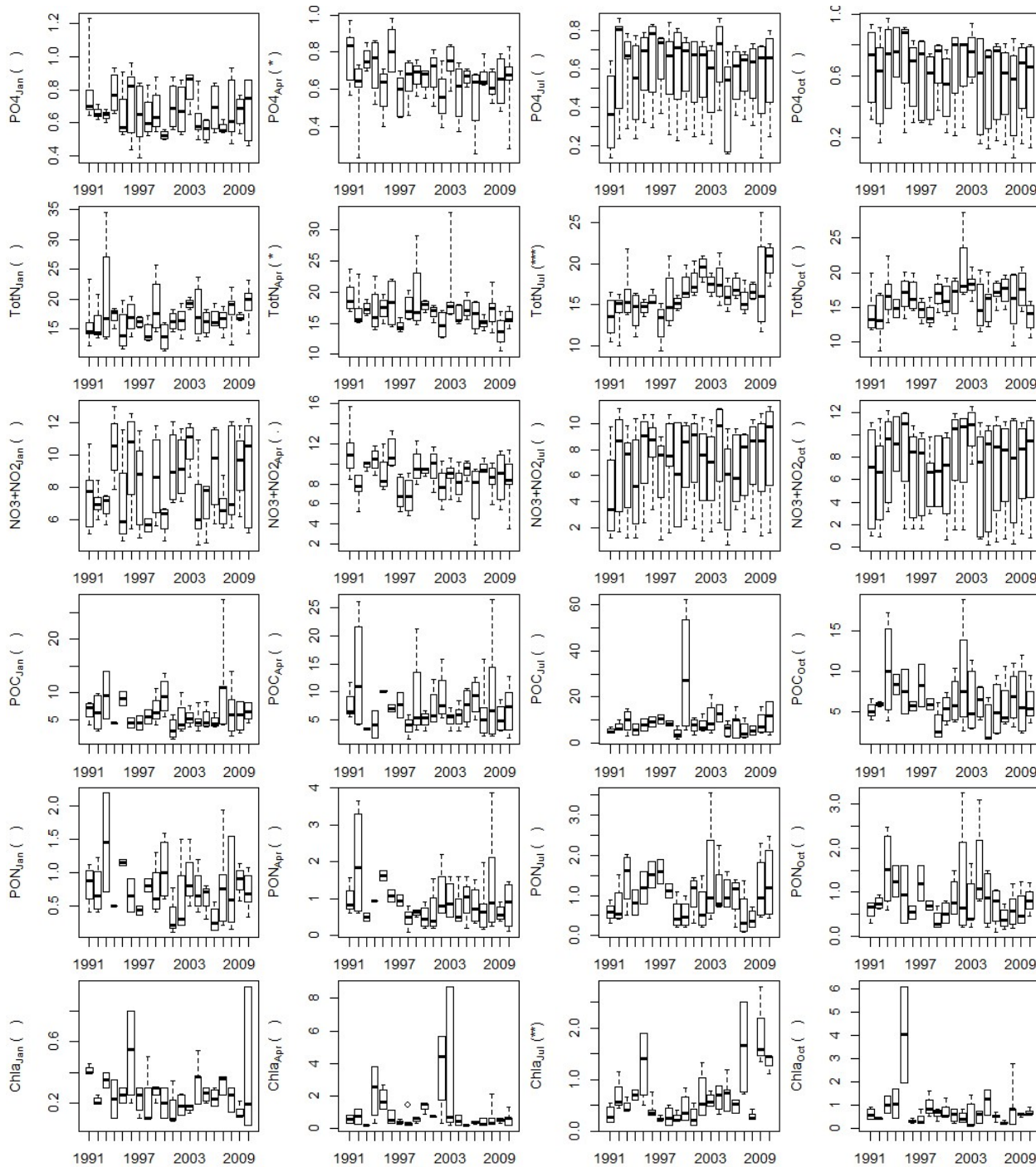
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1059 Figure 7. dbRDA plot of Bray Curtis similarity between samples based on soft bottom data for the period 1991-2010.
1060 Variables identified as significant by DistLM, are typed with red. a) axes 1 and 2, b) axes 1 and 3.

1065 **Supplement 2.** Box (interquartile range) and whisker (extends to the most extreme data points) plots of yearly
 1066 variation in measured environmental variables used in the soft bottom dataset, averaged for all stations. Symbols
 1067 indicate significant levels at <0.001 (***) , <0.01 (**), <0.05 (*), and <0.1 (·) for the regression through time for each
 1068 environmental variable. Pelite content is measured as % particles < 0.063 mm, temperature (T) is given in °C,
 1069 salinity (Sal) in ppt, Total Organic Carbon (TOC) in mg g⁻¹ whereas all nutrients, i.e. total phosphor (TotP),
 1070 phosphate (PO₄), total nitrogen (TotN), nitrate + nitrite (NO₃+NO₂), Particulate Organic Carbon (POC), and
 1071 Nitrogen (PON) are given in μM.
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