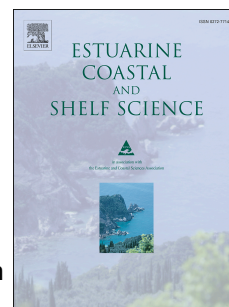


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Three decades of change in the Skagerrak coastal ecosystem, shaped by eutrophication and coastal darkening

Helene Frigstad, Guri S. Andersen, Hilde C. Trannum, Maeve McGovern, Lars-Johan Naustvoll, Øyvind Kaste, Anne Deininger, Dag Ø. Hjermann



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Title:

Three decades of change in the Skagerrak coastal ecosystem, shaped by eutrophication and coastal darkening.

Running Head: Long-term changes Skagerrak ecosystem

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Keywords: biogeochemistry, benthic communities, phytoplankton, climatic changes, coastal darkening, environmental monitoring, Skagerrak.

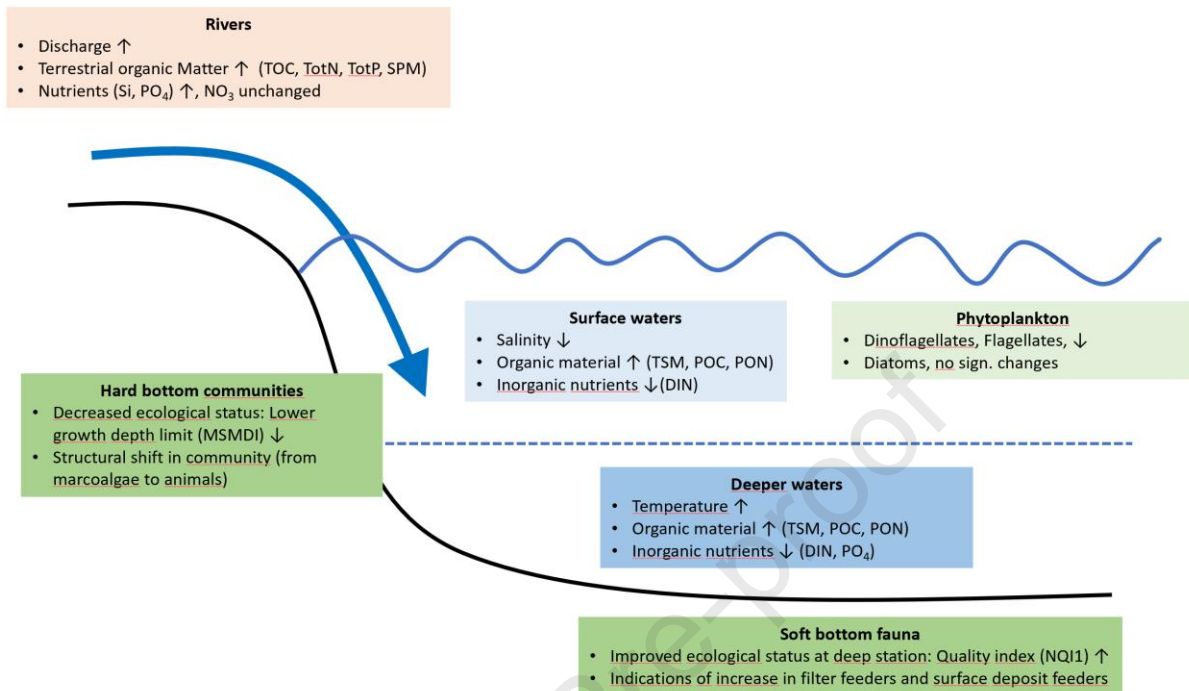
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Abstract

Global coastal ecosystems are under accelerating pressure from human activities and climate change. In this study we explore a long-term time series (mostly 1990-2016) from major Norwegian rivers, together with coastal time series from the Norwegian Skagerrak coast. The aims are to: 1) test long-term trends in riverine loadings to Skagerrak, changes in coastal water quality and pelagic and benthic species composition, and 2) to describe the relationships between human drivers (eutrophication and coastal darkening) and community structure of benthic communities. Riverine discharge and transport increased by 23-85% over the time period, corresponding to a 40-78% increase in concentrations of suspended particulate material in coastal waters and reduced surface salinity, connected to the reported coastal darkening of coastal waters. There was a worsening in ecological status for hard-bottom benthic communities (0-30m) and a reduction in the lower growth depth limit of several macroalgae species. A structural shift in the community composition from macroalgae to increased abundance of animals was found to be related to increased coastal darkening and reduced eutrophication. The concentration of coastal inorganic nutrients (DIN, PO₄) declined by 27-36%, in response to management efforts to reduce eutrophication in European regional seas. Results indicate that reduced eutrophication was related to increased ecological status of the deep soft-bottom community (350m), with a reduction in opportunistic polychaetes and an increase in filter feeding bivalves. This work highlights how climate change and other human-induced changes in a boreal ecosystem intensifies land-ocean interactions, and calls for more adaptive monitoring, where traditional water quality programs and policies evolve iteratively as new information emerges and the major drivers of the systems change.

52

53 **Graphical abstract**

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1. Introduction

Coastal ecosystems are among the most productive global ecosystems (Nixon 1988, Cloern et al. 2014), but are under accelerating pressures from human activities and climate change, with implications for water quality and provision of important ecosystem services (Cloern et al. 2016; Halpern et al. 2008). These transitional zones are uniquely influenced by processes from both land and sea, and their high productivity can in part be attributed to fueling from nutrient run-off from land (Barbier et al. 2011; Cloern and Jassby 2012; Nixon 1988).

Situated in northern Europe, the Skagerrak and North Sea have densely populated catchment areas where human activities have resulted in impacts such as eutrophication, contamination, and marine litter pollution (OSPAR 2017). In addition, these regions experience effects of climate change, such as ocean warming and species displacements (Beaugrand et al. 2014; Perry et al. 2005; Rinde et al. 2017) and ocean acidification (Jones et al. 2018). Historically, eutrophication has been a major concern, and management efforts to reduce riverine loadings of inorganic nutrients has led to improvements in eutrophication status in several coastal areas of the North Sea and Skagerrak over the last three decades (Carstensen et al. 2006; Norderhaug et al. 2016; Trannum et al. 2018; Vermaat et al. 2008). In contrast, concentrations of suspended organic material (dissolved and particulate) have increased in Skagerrak coastal waters over the same time period (Frigstad et al. 2013), hypothesized to be related to increased riverine loads of organic material in boreal freshwaters (de Wit et al. 2016b; Deininger et al. 2020; Solomon et al. 2015) and connected to the reported “coastal darkening” of coastal Skagerrak and the North Sea (Aksnes et al. 2009; Dupont and Aksnes 2013; Opdal et al. 2019).

Climate change is intensifying the coupling between land and coastal ecosystems in many regions, and research across the aquatic continuum (from headwaters to the oceans) has

been identified as one of the major challenges for the next decades (Borja et al. 2020; Canuel et al. 2012; Xenopoulos et al. 2017). Increased understanding of the ability of coastal systems to transform and process carbon and nutrients will help to reduce the uncertainties in the functioning of the global ocean carbon cycle, and is tightly coupled to climate regulation (Friedlingstein et al. 2019).

In this work, we combine long-term datasets (1990-2016) from riverine and coastal monitoring programs in Norway, with the aim to: 1) document and test significance of long-term trends in riverine loadings to Skagerrak, coastal water quality and pelagic and benthic species composition and 2) investigate relationships between changes in human drivers (eutrophication, coastal darkening) and species composition of benthic communities.

2. Materials and methods

2.1. Study area and data description

The Skagerrak is situated in the North-East Atlantic Ocean, between Denmark, Sweden and Norway (Figure 1, see also simplified circulation pattern). The circulation of the surface water is on average cyclonic, and consists of the Jutland Current along the west coast of Denmark, which mixes with the Baltic Current, local river run-off and more saline Atlantic Water from the west to create the Norwegian Coastal Current (NCC; Sætre 2007). The North Atlantic Oscillation (NAO) influences the circulation of water masses in the region, where positive NAO conditions indicate intensified inflow of water masses from the North Sea and Baltic Sea into Skagerrak (Winther and Johannessen, 2006). The Baltic Sea is a major source of freshwater for the NCC (around 75%), while the inflow of saline nutrient-rich waters from the southern North Sea has a large impact on the nutrient status of Skagerrak coastal waters (Aure et al. 1998; Frigstad et al., 2013).

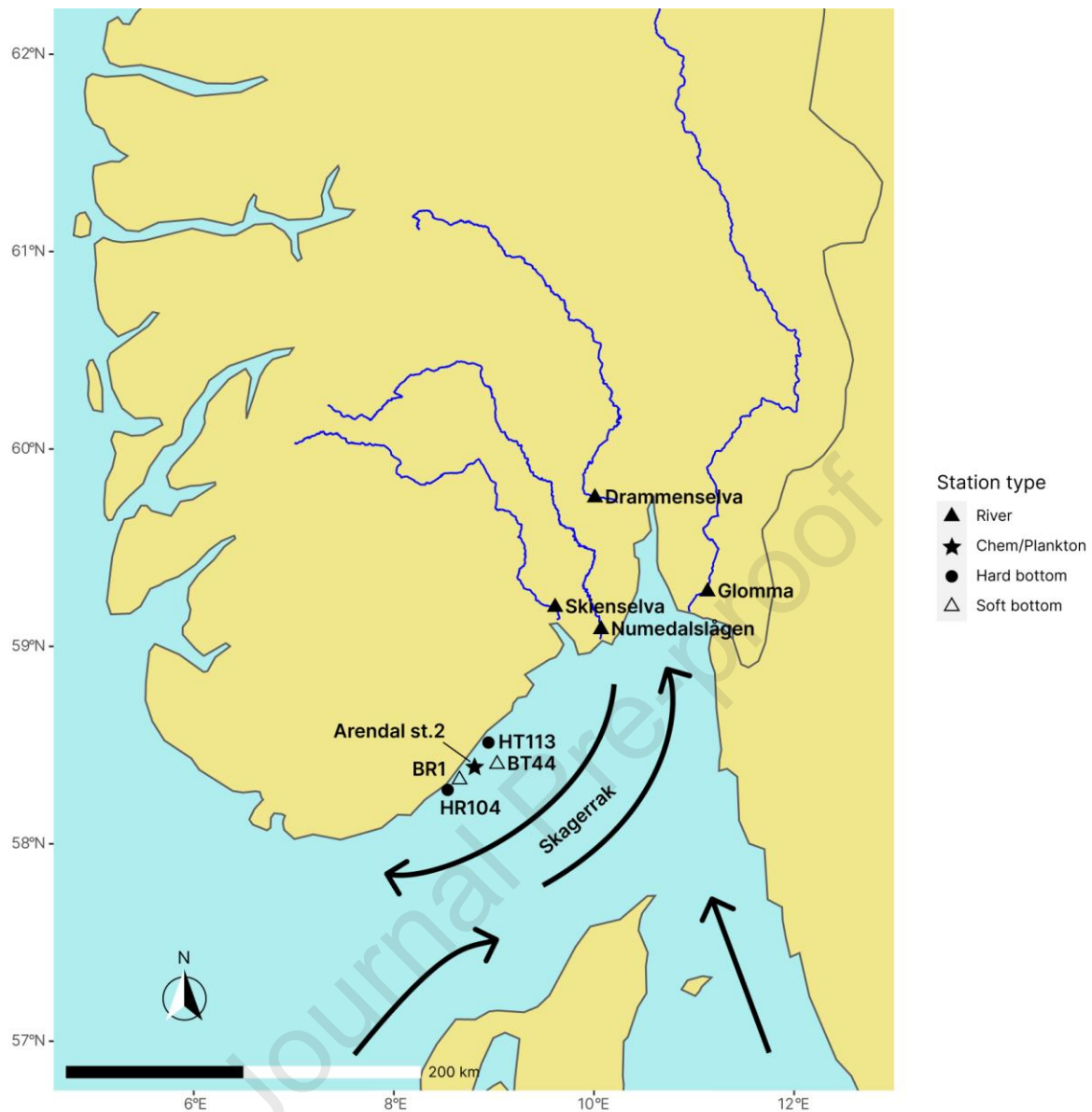


Figure 1. Location of time series stations in Skagerrak, for river stations (filled triangle and river course in blue lines), coastal biogeochemistry (abbreviated to “Chem”) and plankton station (filled star), hard bottom stations (filled circles) and soft bottom stations (open triangle). Arrows indicate a simplified circulation pattern in Skagerrak.

The long-term datasets included in this study (see location of stations in Figure 1 and overview in Table 1) are part of the Norwegian river monitoring program (Kaste et al. 2018), and the Ecosystem monitoring of Norwegian coastal waters (ØKOKYST; Moy et al. 2017), both funded by the Norwegian Environment Agency.

Table 1. Overview of time series stations

Data type	Stations (positions)	Sampling depth(s)	Frequency	Time period
Rivers	Glomma (59.28°N 11.13°E), Drammenselva (59.75°N 10.01°E), Numedalslågen (59.10°N 10.07°E), Skienselva (59.20°N 9.61°E)	Surface	Monthly	1990-2016
Coastal biogeochemistry	Arendal st. 2 (58.39°N 08.83°E)	0,5,10,20,30, 50,75m	Biweekly (Mar-Sep), monthly	1990-2016
Phytoplankton		5m (1994-1999: 0-30m), 0-30m (transect)		1994-2016
Hard-bottom communities	Prestholmen – HR104 (58.27N 08.54E), Tromøy - HT113 (58.51N 08.94E)	0-30m (transect)	Annually (May/Jun)	1990-2016
Soft-bottom Fauna	Grimstad - BR1 (58.33N 08.63E), Arendal – BT44 (58.40N 09.03E)	50m, 350m	Annually (May/Jun)	1990-2016

The major Norwegian rivers draining to Skagerrak (see Figure 1 and Table 1) are (catchment sizes in parenthesis): Glomma (41918 km²), Drammenselva (17034 km²), Numedalslågen (5577 km²), and Skienselva (10772 km²). Measured chemical parameters included; nitrate (NO₃), total nitrogen (TotN), phosphate (PO₄), total phosphorus (TotP), total organic carbon (TOC), suspended particulate matter (SPM) and silicate (SiO₂). Daily discharge data provided by the Norwegian Water Resources and Energy Directorate (NVE) were used to calculate element transport. More information on procedures and methods are described in Kaste et al. (2018).

The coastal biogeochemistry and phytoplankton data sets are from northern Skagerrak (see Figure 1 and Table 1) and the Arendal st. 2 is located one nautical mile off the coast off Norway at approx. 105 m depth, see Moy et al. (2017) for detailed information on methods and procedures. Measured biogeochemical parameters included: temperature, salinity, oxygen, Secchi depth, dissolved inorganic nitrogen (DIN), phosphate (PO_4), silicate (SiO_2), total nitrogen (TotN), total phosphorus (TotP), Chlorophyll *a* (Chl*a*), particulate organic carbon (POC), particulate organic nitrogen (PON), particulate organic phosphorus (POP) and total suspended matter (TSM). Observations of TSM were missing for the period 2012-2013, so these values were interpolated using the zoo package in R (Zeileis and Grothendieck 2005). Measurements of POC, PON, POP and DIN in the deep layer (50 and 75m) ended in 2013. Phytoplankton were analyzed according to the Utermöhl method (Sournia 1978), following the Norwegian standard (NS-EN 15972:2011), using an inverted light microscope. Identification to species level was not possible to achieve systematically for the whole time period, so to harmonize datasets from different years for, species data was aggregated into three main phytoplankton groups (diatoms, dinoflagellates and flagellates), and the species lists were therefore not included in the ordinations and regression analyses.

The hard-bottom datasets are from dive transects conducted annually on two stations (HR104 and HT113; see Figure 1 and Table 1). The surveys were conducted from a maximum depth of 30 m and up to the surface. Dive transects were performed to obtain semi-quantitative registration of abundance of macroalgal and faunal species (or taxa) (see Norderhaug et al. (2015) for further descriptions). The Multi Species Macroalgae Depth Index (MSMDI) serves as an indication of eutrophication and increased concentrations of particulate matter in the water column (Blomqvist et al. (2012). It is based on the lower growth depth (in m) of nine macroalgal species known to respond to reduced light conditions and estimated as the maximum depth to which abundance was recorded as scattered or denser each year. For

Skagerrak, the species are *Chondrus crispus* (irish moss), *Coccotylus truncatus*, *Delesseria sanguinea* (sea beech), *Furcellaria lumbricalis* (clawed fork weed), *Halidrys siliquosa* (pod weed), *Phycodrys rubens* (sea oak), *Phyllophora pseudoceranoides* (stalked leaf bearer), *Rhodomela confervoides* (straggly bush weed) and *Saccharina latissima* (sugar kelp). From the MSMDI-index the Ecological Quality Ratio (EQR) was calculated, which is presented on a numerical scale from zero to one (unitless), where a value of one indicates very good ecological status which is close to reference (pristine) conditions and values of zero indicates very poor ecological status. The procedure is described in the Norwegian handbook for classification according to the Water Framework Directive (WFD) and the MSMDI-index is used as the Biological Quality Indicator for hard-bottom communities in determining ecological status in Norwegian coastal waters (Norwegian Classification Guidance 2018). The species diversity was calculated by the Shannon–Wiener index (Shannon and Weaver 1963) using the logarithm base of 2 (H'). The Pielou's evenness index (J') was calculated by dividing the Shannon-Wiener index (H') by the species richness (Pielou 1966). The Shannon-Wiener index reflects the number of species in the dataset (richness), simultaneously taking into account how evenly the basic entities (individuals) are distributed among those types. The Pielou's evenness index ($0 - 1$, unitless) refers to how evenly total abundances are distributed across taxonomic groups. Low evenness (J) indicates higher variability in abundances among groups and/or the presence of a dominant species or group.

The soft-bottom fauna were sampled on two stations (BR1 and BT44; see Figure 1 and Table 1) using a 0.1 m^2 grab and the fauna $> 1 \text{ mm}$ were collected. The field work and processing were performed according to NS-EN ISO 16665:2013. All organisms were identified to species or lowest taxon possible. Across the time series, either four or eight grabs were sampled, but for the purpose of the present work, four grabs were used, and all values were averaged per 0.1 m^2 . We calculated the species diversity indices Shannon-Wiener (H')

and Norwegian Quality Index (NQI1; Molvær et al. 2009). The NQI-index (calculated as the EQR value from 0-1, see above) is used as one of the Biological Quality indicators for classifying ecological status of soft-bottom fauna in Norwegian coastal waters as part of the WFD (Norwegian Classification Guidance 2018). The stations were also sampled for percent sediment fine fraction (i.e. % particles < 63 μ m) and Total Organic Carbon (TOC, mg/g). For more detailed descriptions of the methodology, see Trannum et al. (2018).

2.2. Statistical analyses

All statistical analyses were performed using the R statistical software (R CoreTeam 2018), and plots were made using the ggplot2 package (Wickham 2016). Time series with monthly (or higher resolution) sampling were aggregated into annual averages, using the monthly mean values for coastal biogeochemistry and plankton and the monthly summed values for the four rivers. For the coastal biogeochemistry, we aggregated into surface (0, 5, 10m), intermediate (20, 30m) and deep (50, 75m) depth layers.

A non-parametric Mann-Kendall test was applied to test for a significant monotonic time series trend in all variables in the coastal biogeochemistry, plankton and river datasets, in addition to selected quality indices (MSMDI and NQI1) for benthic communities (Mann 1945). The test was applied on the annually aggregated data, using the rkt package in R (Marchetto 2017), and the results are visualized in Figure 3 and summarized in Table A1. Time series of selected variables are shown in Figures 4 to 7 (showing the annual aggregate with a Loess smoothing function with a span of 0.7 for all variables).

Detrended correspondence analysis (DCA) (Hill and Gauch 1980) was performed using the vegan package in R (Oksanen et al. 2018) to produce ordination diagrams for the hard- and soft-bottom species data. The main ordination axis was highly correlated with time, and therefore the species scores were also viewed in relation to time in our analyses. The species

with the most extreme scores on either end of the main ordination axis (DCA1, Figures 6 and 7) represent the most distinct differences between the start and the end of the monitoring period (cf. Figures A3-A7). For the hard-bottom dataset one analysis comprising both stations was performed, while for the soft-bottom datasets each station was treated separately, based on the knowledge that there are distinct differences in species composition between the two sites (Trannum et al. 2018).

We used structural equation modelling (SEM) to test potential causal relationships between river discharge, coastal biogeochemistry and benthic community composition and status for the coastal Skagerrak system.

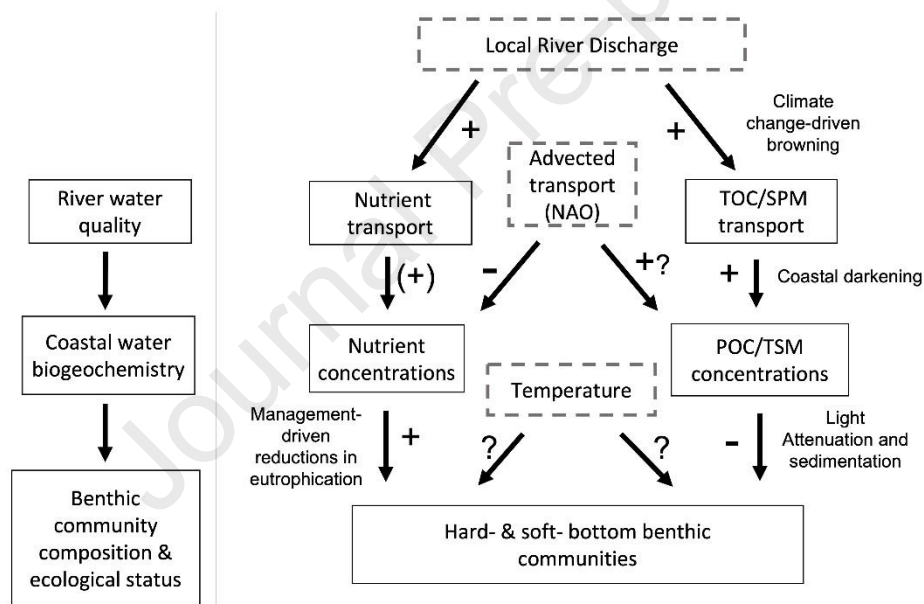


Figure 2. Conceptual diagram linking coastal darkening and recovery from eutrophication to coastal biogeochemistry and hypothesized impacts on hard and soft bottom benthic communities.

SEM was carried out using the lavaan package in R (Rosseel Y, 2012) using the variables selected through conceptual discussions (Figure 2) and results of the Mann-Kendall tests

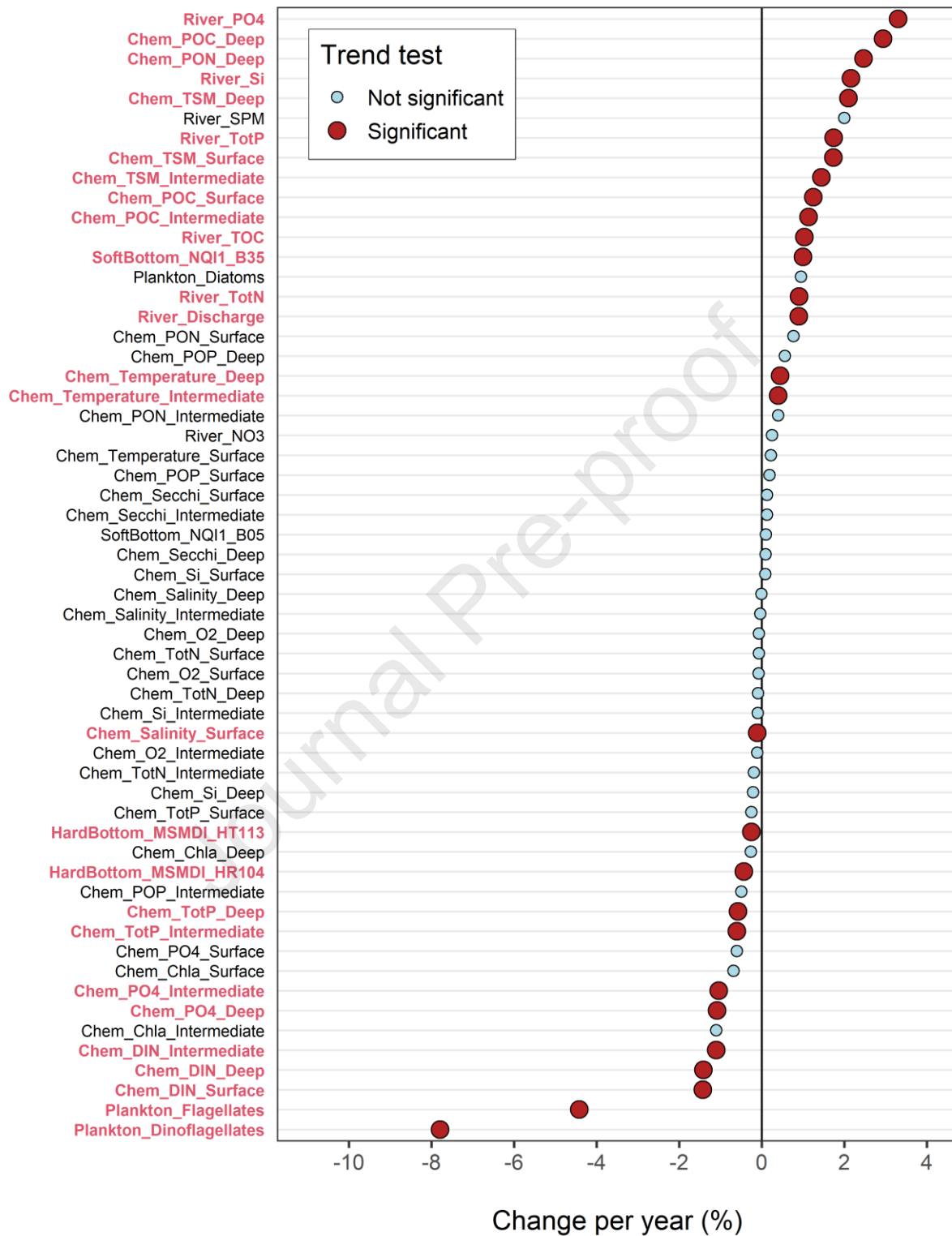
(Figure 3). Structural equation modeling tests the path significance among variables in the model (significant when $p < 0.05$) as well as the overall significance of the model structure (significant when $p > 0.05$). Structural equation modeling was applied using a covariance matrix calculated from scaled annual data, which were further centered and standardized automatically during the analysis so that resulting coefficients in the structure are directly comparable. Local river discharge and strength of the advected water signal (represented by winter NAO index) were included as drivers of coastal water biogeochemistry. Principal component analysis was carried out in the R package ‘vegan’ on coastal water biogeochemical parameters grouped by eutrophication-associated variables (DIN and PO₄) and coastal darkening-associated variables (TSM and POC). PCAs were built using both surface and intermediate depth measurements, which were scaled prior to analysis. The first PC axes (representing 67 % and 76 % of the variance for each group respectively), were extracted and used in the SEM to connect drivers (river discharge, advected waters (NAO), temperature) to changes in benthic communities. Hard and soft bottom benthic communities were represented by the DCA axes constructed for each station individually. We hypothesized that coastal darkening and recovery from eutrophication would have different impacts on the deep soft bottom station compared to the shallow soft bottom station and the two hard bottom stations. Thus, in the SEM model, the first DCA axes from each of the hard bottom stations (HR104, HT113), and the shallow soft bottom station (BR1) were grouped in one latent variable while the deeper soft-bottom station (BT44) DCA axis was kept separate.

3. Results

3.1. Time series trends

Mann-Kendall tests (Figure 3) showed that around half of the variables tested changed significantly over the time period 1990 – 2016 (summary of test statistics given in Table A1).

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240 Figure 3. Mann-Kendall trend tests for annually aggregated data for river (River), coastal

241 biogeochemistry (Chem) and phytoplankton (Plankton), as well as the MSMDI-index for hard-bottom

macroalgae (HardBottom) and the NQI-index for soft-bottom fauna (SoftBottom). The trends (Theil-Sen slope) are given in percentage change in the mean quantity per year. Red dots and red bold types indicate significant trends (Mann-Kendall trend test, $p < 0.05$). The numbers are given in Table A1.

For the Norwegian rivers draining to Skagerrak, there were significant upward trends for discharge and transport of PO_4 , Si, TotP, TOC and TotN (between 1-3% increase per year), while no significant trend was found for NO_3 (Figure 3). There was a flood event in 2000 (Figure 4), with high discharge and transport of NO_3 , Si, SPM, TOC and TotN. There were large variations in discharge among the rivers, with Glomma being approximately one order of magnitude higher than Numedalslågen, Skienselva, and Drammenselva, however the trends in element transport are largely similar (Kaste et al. 2018). The seasonal variations in element transport were largely driven by the variation in river discharge, causing the flow volumes to be generally 1.5-2 times higher in spring (May-July) compared to the other seasons (data not shown). This period captures the flood events related to snow melt in Glomma and Drammenselva that generally occur in May, and result in correspondingly increased transport of TOC, NO_3 , TotN and TotP during this period (Kaste et al. 2018).

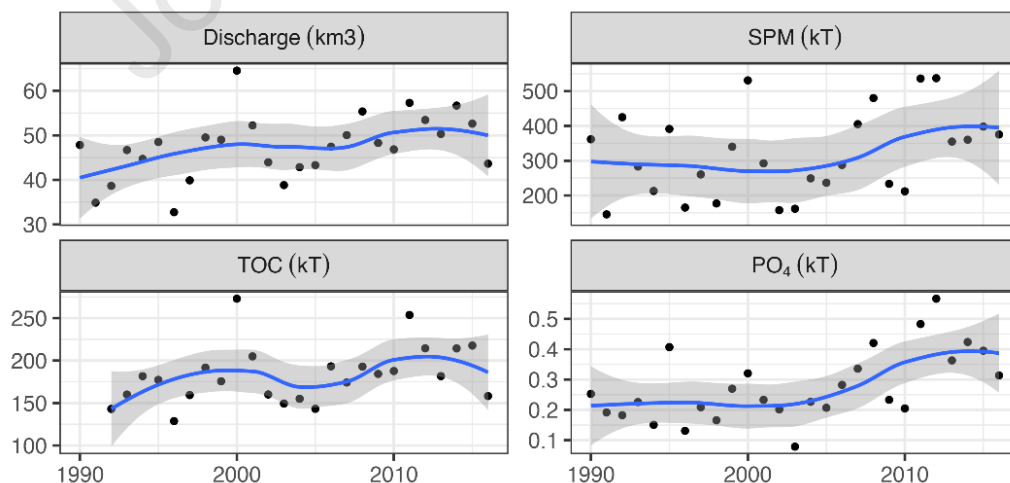


Figure 4. Total discharge (km^3) and transport of NO_3 , PO_4 , Si, SPM, TOC, and PO_4 (all in ktonnes) summarized for major rivers draining to Skagerrak (Glomma, Drammenselva, Numedalslågen and

Skienselva). Black dots indicate the annual sums and the blue line represent the Loess smoothing function (shaded area shows the SE).

For coastal biogeochemistry, the variables with the largest upward trends across the time series were POC, PON and TSM concentrations, with the largest increase observed in the deep layers (around 2-3% per year; Figure 3). The highest absolute concentrations of POC and PON were found in the surface layer of around $17 \mu\text{mol L}^{-1}$ and $2 \mu\text{mol L}^{-1}$, respectively, towards the end of the time period (Figure 5A). The TSM concentrations were more uniform across the water column, with concentrations between 0.8 and 1.2 mg L^{-1} . The temperature also increased significantly over time in the deep and intermediate layers (in total $\sim 1^\circ\text{C}$ over the time period; Figure 3), while there was no significant change in the surface layer, which showed higher interannual variations (Figure 5A). There was a significant downward trend in salinity in the surface layer over time (from >29 to $27-28$), while there were no significant changes in the salinity of the intermediate (~ 33) and deep (~ 34) layers (Figure 3 and Figure 5A). The largest significant downward trends were observed for the DIN and PO_4 concentrations (Figure 3), between 0.5 and 1.5% per year. The DIN concentrations had the largest percentage decrease over time for all depths, however, there was a transient increase in concentrations at the start of the monitoring period (with maximum of $>7 \mu\text{mol L}^{-1}$ around 1995 in the deepest layer), followed by decrease towards the end of the time period ($\sim 3 \mu\text{mol L}^{-1}$ in surface layer; Figure 5A). The reduction in PO_4 concentration was more uniform over time and reached $\sim 0.4 \mu\text{mol L}^{-1}$ in the deep layer towards the end of the time period (Figure 5A), with the largest percentage and significant decrease in the intermediate and deep layers (Figure 3). There were downward trends in the Chla concentrations in all depth layers, however these were not significant ($P=0.05$ in the intermediate layer, Figure 3), except for Chla concentrations during the fall period (August to October, data not shown). The Chla concentrations ranged from 0.5 to $2 \mu\text{g L}^{-1}$ in the surface and intermediate layers (Figure 5A). Similarly, no significant time trends were

detected for the Secchi depth observations (Figure 3). The time series of Secchi depth observations were dome-shaped (Figure 5A), with around 8-9m on an annual average at the start of the time period, shoaling down to between 6-8m around 2000, but increasing after 2010 to similar levels as in 1990.

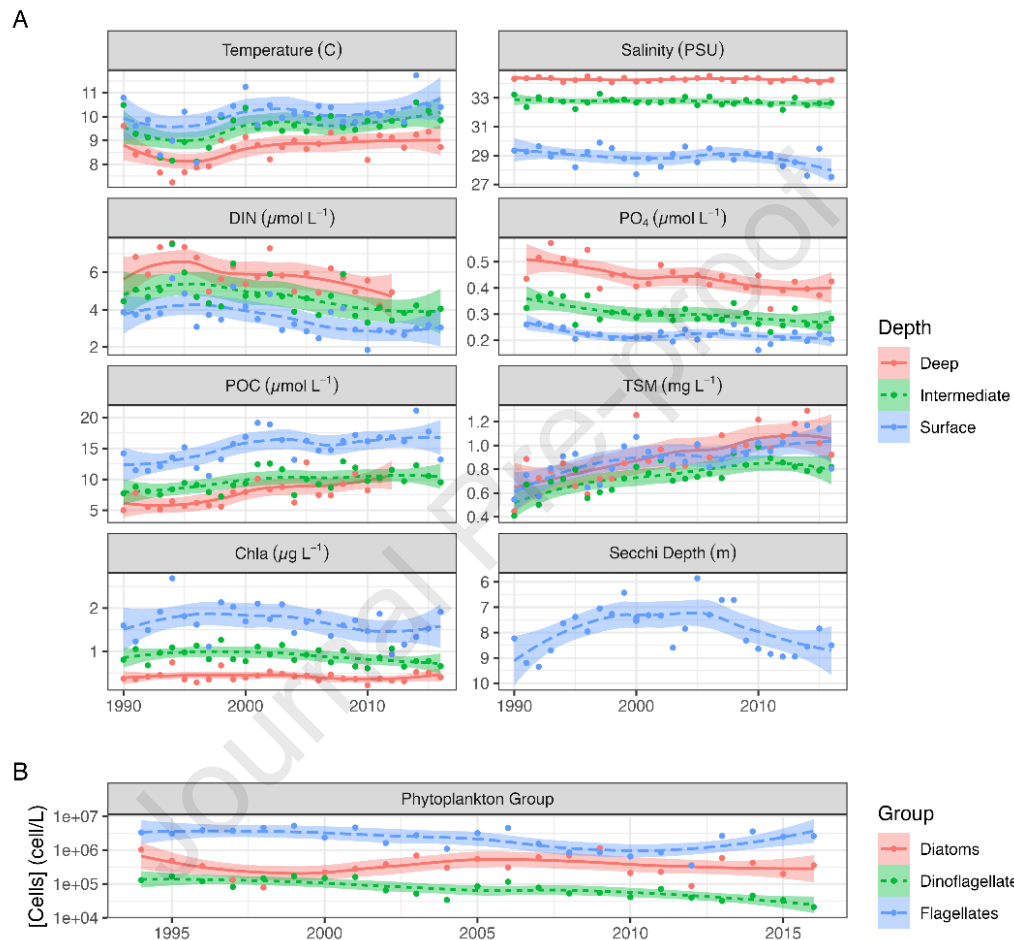


Figure 5. Time series of (A) temperature, salinity and DIN, PO_4 , POC and TSM for surface (0-10m, in red), intermediate (20-30m, in green) and deep (50-75m, in blue) and (B) Abundances of diatoms (red), dinoflagellates (green) and flagellates (blue; all in cell L^{-1}) at the Arendal st. 2. Dots indicate the annual averages and lines represent the Loess smoothing function (shaded area shows the SE).

The largest downward trends among all variables tested were found for the flagellates and dinoflagellates (10 and 8 % decrease per year, respectively), while there was no significant change for diatoms (Figure 3). For dinoflagellates there was a steady reduction in abundance

(cell L⁻¹) over time (Figure 5B). The diatom and flagellate groups showed larger interannual variation (Figure 5B), where there were marked changes in abundance in the first and last part of the monitoring period, respectively.

The macroalgal index based on lower growth depth (MSMDI) had significant downward trends at both stations, indicating decreased ecological status in the hard-bottom communities over time (Figure 3), where one of the hard-bottom station (HR104) decreased from “good” to “moderate” ecological status towards the end of the time period (Figure 6A). The lower growth depth limit of the nine macroalgae species included in the MSMDI-index has generally become shallower over time (Figure 6B), with a reduction of between 1.2 to 3.8m in the lower growth limit for *Saccharina latissimi* (sugar kelp) over the time period. There were also structural changes in species composition of hard-bottom communities over time (Figure 6A), where the number of macroalgal species reached a maximum before year 2000 and decreased markedly towards the end of the time period. The number of faunal species increased over the time period, with some interannual variation. The overall species richness was higher in 2016 than the early 1990s, but has decreased since around year 2000. Both diversity indices (H' and J') peaked between year 2000 and 2005, meaning that species diversity was highest, and the presence of dominant species was less prominent in this period. The overall shift in species composition was a shift from more algal species towards more faunal species, with minor changes in the evenness (i.e. the dominance-structure; J') within the community.

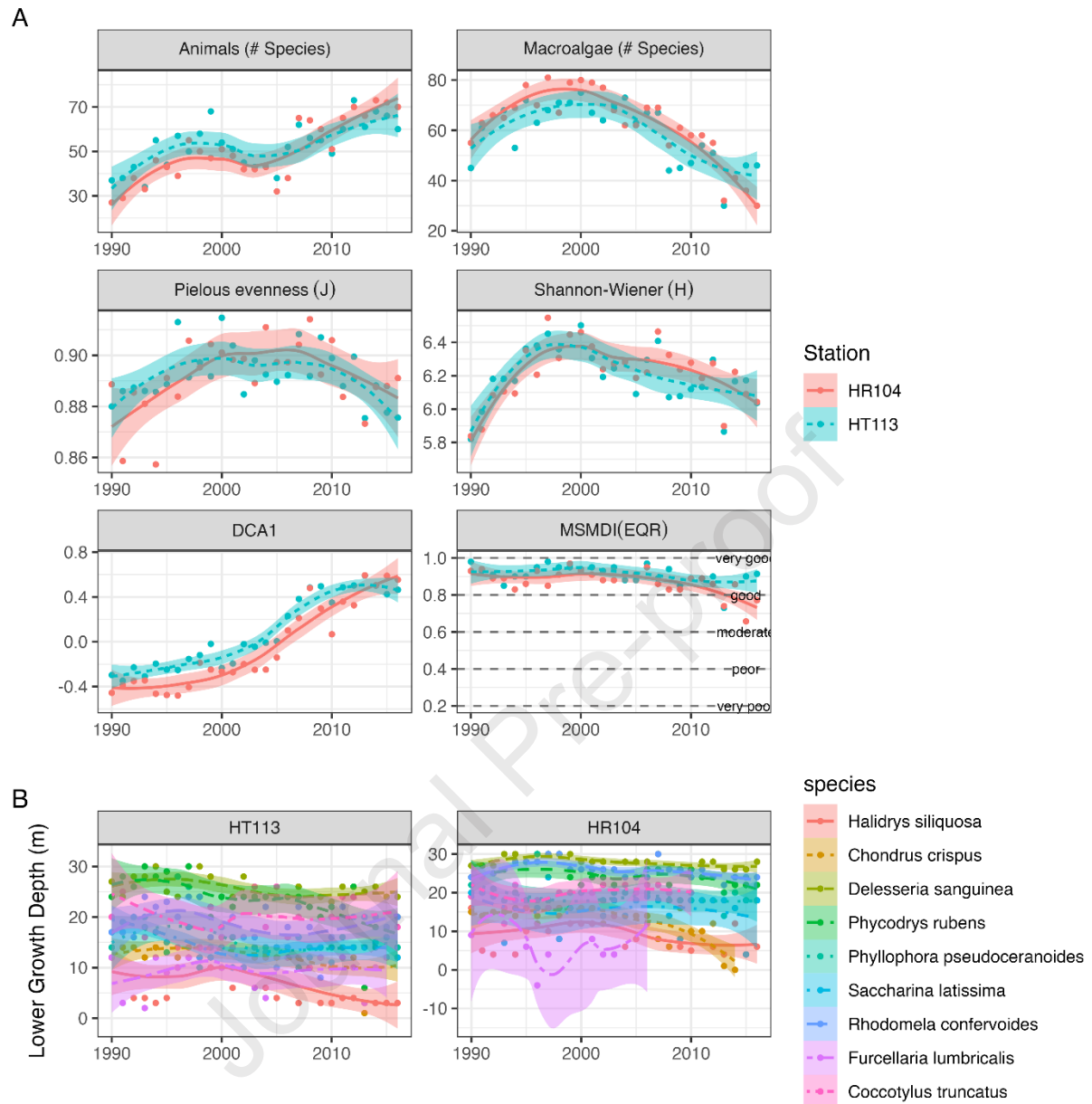
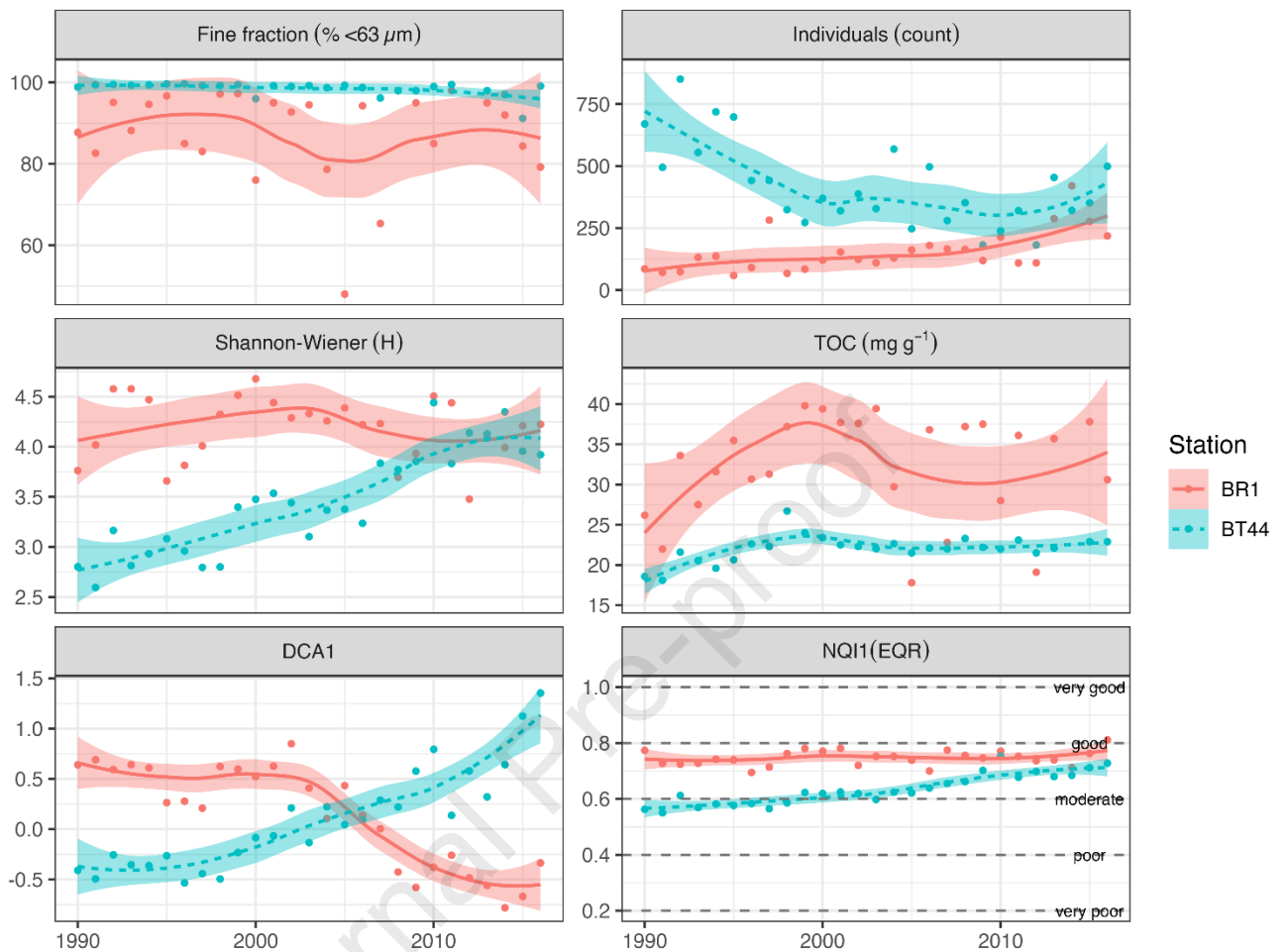


Figure 6. (A) Time series of hard-bottom groups of animals and macroalgae (no. of species), the species diversity indices Shannon-Wiener (H'), Pielou's evenness (J'), DCA1 and the MSMDI-index (EQR) for the hard-bottom stations HR104 (Prestholmen; red) and HT113 (Tromøya N; blue). Dots indicate the annual values and lines represent the Loess smoothing function (shaded area shows the SE). For MSMDI, horizontal dashed lines refer to ecological status (0.8 - 1 = very good, 0.6 - 0.8 = good, 0.4 - 0.6 moderate, 0.2 - 0.4 poor, 0 - 0.2 very poor). (B) Lower growth depth (m) for 9 species of macroalgae at each station.

For the soft-bottom communities, there were marked differences between the shallow (BR1) and the deep (BT44) station over the period from 1990 to 2016. In the deeper waters (BT44), there was a significant upward trend in the NQI1-index (Figure 3), indicating an improvement in ecological status from “moderate” to “good”, also shown by the increase in the species diversity index (H') and a reduction in the number of individuals and increased species number (Figure 7). The number of species also increased at the shallow station (BR1), but as the number of individuals also increased, there was no accompanying increase in the diversity indices (Figure 75). Sediment TOC concentrations were higher at the shallow (BR1) station, and for both stations there were elevated concentrations around year 2000 (especially at the shallow station), but with no clear overall changes over the time period. No large changes in the sediment grain size (fraction of fine sediments; %<63 μ m) were observed over the time period, suggesting that the sediment composition itself did not change. The deep station (BT44) had stable values of TOC and fine fraction over time, while there were larger variations for the shallow station (BR1).

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340 Figure 7. Time series of the number of species and individuals, the species diversity indices Shannon-
 341 Wiener (H') and NQI1, the concentration of TOC (mg/g) and fraction of fine sediments ($\% < 63 \mu\text{m}$),
 342 DCA1 and NQI1 for the soft-bottom stations BR1 (Grimstad, 50 m; red) and BT44 (Arendal, 350 m;
 343 blue). The biological parameters are mean values of four grabs. Dots indicate the annual values and
 344 lines represent the Loess smoothing function (shaded area shows the SE). For NQI1, dashed gray
 345 horizontal lines refer to ecological status (0.8 - 1 = very good, 0.6 - 0.8 = good, 0.4 - 0.6 moderate, 0.2
 346 - 0.4 poor, 0 - 0.2 very poor).

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348 3.2. Relationships between drivers and observed responses

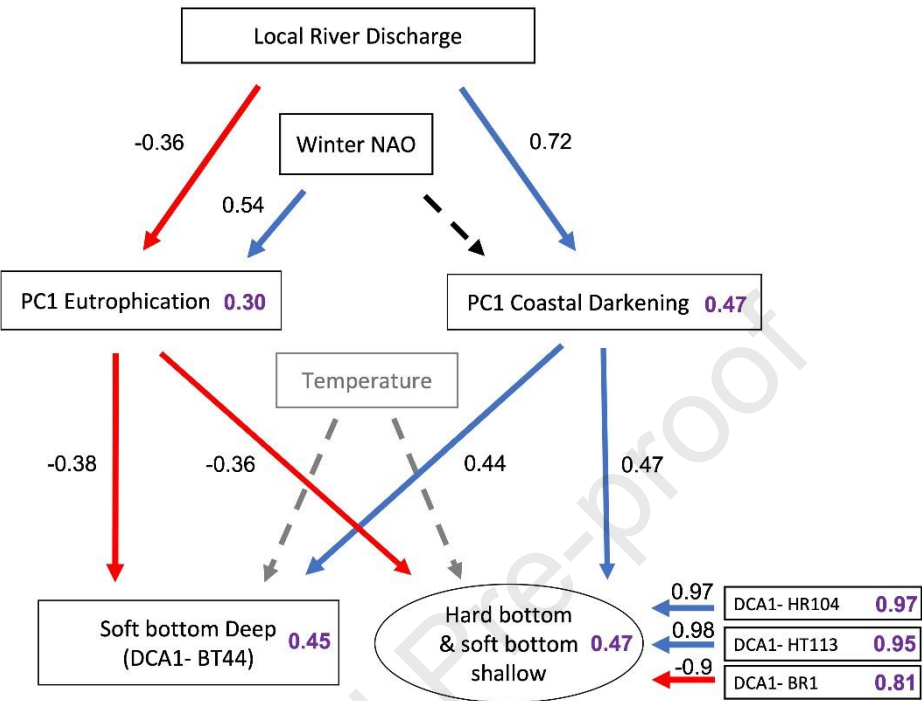
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Structural equation modelling (SEM; see Section 2.2 for details and conceptual diagram) was used to connect drivers of coastal change (river discharge, strength of advected water (winter NAO-index) to coastal biogeochemistry (variables associated with eutrophication and coastal darkening) and, subsequently, to changes in coastal hard and soft bottom benthic communities. Adjustments were made to the model to achieve better model fit, including the removal of bottom water temperature as a driver of change in hard- and soft-bottom communities. Model fit indices were significant, confirming that the data sufficiently match the proposed conceptual diagram ($\chi^2 = 16.98$; $P = 0.257$; $df = 14$; $CFI = 0.982$, $TLI = 0.964$, $RMSE = 0.092$).

Coastal water biogeochemistry, grouped by variables associated with eutrophication and coastal darkening, were represented by PC axes, both of which increased with increasing concentrations of dissolved and particulate matter, respectively. Thus, results indicate that increases in local river discharge are related to reduced eutrophication but increased coastal darkening of Skagerrak coastal waters. Meanwhile, the strength of the advected water signal (NAO-index) was positively related to eutrophication, but had no significant relationship to coastal darkening over the time series.

The SEM results reveal positive relationships between coastal darkening and soft and hard bottom DCA axes, and negative relationships between coastal eutrophication and DCA axes. For hard-bottom communities, the main ordination axis (DCA1) shows that the species composition changed over time, with gradual change in the 1990s, before more rapid changes occurred from around 2000 for (see left panel in Figures 6 and 7, respectively). These changes are associated with a decrease in macroalgal species, and an increase in animals (Figures A3 & A4). Meanwhile, for the deep soft-bottom community (BT44), there were

374 more consistent changes in the community structure over time, with a decrease in
375 opportunistic polychaetes and an increase in filter-feeding bivalves (Figure A6)



376
377 Figure 8. Structural equation model (SEM) linking increases in river discharge and advected
378 water transport (NAO index) to coastal eutrophication and darkening and, in turn, community
379 structure of hard and soft bottom benthic communities (DCA axes) in coastal Skagerrak. Latent
380 variables are represented as ellipsoids, and measured variables as rectangular boxes. The PC
381 axes are composed of DIN and PO4 for eutrophication and TSM and POC for coastal
382 darkening, collected at surface and intermediate depths in the water column. Positive
383 directional pathways are depicted in blue and negative pathways in red. Coefficients for
384 significant pathways ($p < 0.05$) are included beside the arrows and represent the rate at which
385 the response variable changes in response to a change in its predictor. Nonsignificant pathways
386 are shown in black, and pathways that were tested but not included in the final model are shown
387 in gray. Variance explained (R^2) is included (in purple) for endogenous variables. Model fit:
388 ($\chi^2 = 16.98$; $P = 0.257$; $df = 14$; CFI = 0.982, TLI: 0.964, RMSE = 0.092).

4. Discussion

4.1. Links between riverine transport and coastal suspended material

The largest upward trends observed for the coastal water masses were for the suspended particulate matter (POC, PON and TSM), with concentrations increasing between 40-78% for the various depth layers from 1990 to 2016. Correspondingly, the riverine discharge and transport increased between 23-85% over the same time period. The connection between these two large-scale trends has been hypothesized in several studies from the Baltic Sea and the larger North Sea, where increased transport of organic material from land leads to increased organic carbon concentrations and enhanced light attenuation in coastal waters (Aksnes et al. 2009, Anderson et al. 2018; Frigstad et al. 2013). In the present study, this link is corroborated where we found significant SEM paths linking local riverine discharge to the long-term increase in coastal POC and TSM concentrations in coastal Skagerrak. Meanwhile, no significant link was found for between the NAO and coastal darkening. Positive NAO conditions is known to intensify the inflow of water masses from the North Sea and the Baltic Sea into Skagerrak (Winther and Johannessen, 2006), where large-scale coastal darkening has also been reported. Even though no significant relationship was found between coastal darkening and the NAO in this study, it is plausible that there could be an increase in organic material and freshwater fraction in the waters advected from the North Sea and the Baltic Sea into Skagerrak, which should be investigated in future studies.

In general, higher loads of terrestrial material (especially terrestrial derived humic material) is connected to higher light attenuation in coastal waters (Jerlov 1976). Over the 20th century, there has been observed decreased Secchi depths and increased light attenuation in the

larger North Sea (including Skagerrak) and the Baltic Sea in several studies (Aksnes et al. 2009; Opdal et al. 2019; Sandén and Håkansson 1996). Several of these studies refer to the increase in riverine DOM concentrations in boreal regions (de Wit et al. 2016; Larsen et al. 2011, Deininger et al. 2020), and state that the driver is likely to be terrestrial inputs of colored dissolved organic matter (cDOM; Aksnes et al. 2009; Capuzzo et al. 2015; Opdal et al. 2019). Both organic and inorganic TSM have also been identified as potential contributors to the long-term increase in light attenuation (Capuzzo et al. 2015), especially in shallow regions of the North Sea (Opdal et al. 2019). However, the observed increased light attenuation for the majority of studies cited above were on a centennial time scale, while in this study, which investigates the decadal time scale, there was no significant long-term trend for Secchi depth. The pattern of annual average Secchi depth observations over the 26-year time series was dome-shaped, with shallower Secchi depths (around 7.5m) in the middle of the time period from around 1995-2005. There were large floods in the river Glomma in both 1995 and 2000 (Kaste et al., 2018), which could have contributed to the lower Secchi depths observed in this period. The dinoflagellate group had the largest percent change of all variables in this study (around 8% pr year; Figure 3), and the abundances were around 3.5 to 4 times higher at the start of the time series compared to the end. A long-term reduction in dinoflagellate abundance is also shown for the open North Sea and Northeast Atlantic, related to increasing surface temperatures and summer wind (increased turbulence) favoring diatoms over dinoflagellates (Hinder et al. 2012). The substantial long-term reduction in dinoflagellates (with generally compact carbon-rich cells; Menden-Deuer and Lessard 2000), together with the overall reduction in Chla (albeit not significant), could have contributed to counteract the effect of increased light attenuation due to increased coastal TSM and POM concentrations in the Skagerrak. While a detailed study on the controls and contributions to Secchi depth is outside the scope of the present work, more research is needed to understand the interacting factors

determining the long-term changes in light attenuation and ultimately Secchi depth observations in these optically complex coastal waters (Harvey et al. 2019).

The increase in terrestrial organic matter concentration in freshwaters (lakes, streams and rivers) over the last decades in boreal and Arctic regions (termed freshwater browning; Creed et al. 2018; Solomon et al. 2015) is largely due to an increase in the dissolved fraction (DOM), whereas the particulate fraction in riverine waters is comparably low (Gundersen et al. 2019). The drivers might vary both with time and region, but important contributing factors to freshwater browning are reduced atmospheric sulphur deposition, increased precipitation and changes in vegetation (de Wit et al. 2016a; Monteith et al. 2007; Deininger et al., 2020, Kritzberg, 2017). The total or dissolved fraction of organic carbon (DOC or TOC) is not routinely monitored in Norwegian coastal waters. Thus, a direct comparison between riverine and coastal dissolved organic pools is not possible, even though it has been found to be closely related in the upstream outer Oslofjord region (Frigstad et al. 2020). A plausible mechanistic link between the increases in riverine dissolved material and coastal particulate material is through salinity-induced flocculation, where terrestrially derived humic dissolved organic material aggregates to larger sized particles when it crosses a salinity gradient (Buffle et al. 1998; Sondergaard et al. 2003). This flocculation process can create particles that are larger than the operational definition for particulate organic matter (i.e. retained on GF/F-filter with nominal pore size 0.7 μm), and is an important part of the coastal filter whereby riverine organic matter flocculates to larger particles and potentially sinks to the sediments. This process also influences the quality of the remaining DOM pool (e.g. the colored and fluorescent fractions of DOM) and is dependent on regional variations in catchment properties (Asmala et al. 2014; Massicotte et al. 2017). In this study, we found the largest upward trends in suspended material (POC, PON, TSM) for the deep and intermediate layers, where the surface

concentrations were the most significant explanatory variables, indicating that sinking of organic material from the surface layer was the main source.

4.2. Long term changes in benthic communities driven by coastal darkening and reduced eutrophication

Ecological status for the two hard-bottom stations decreased over time, as indicated by a reduction in the lower growth depth limit of several of the nine macroalgae species included in the MSMDI-index, which is a strong indicator of reduced light availability (Blomqvist et al. 2012). Changes in the lower growth depth of macroalgae is also influenced by temperature, whereby increased temperature leads to increased metabolism, which in turn demands more energy. To meet this demand, more light and/or more efficient photosynthesis is required and the ability of macroalgae to regulate photosynthesis is limited under temperature stress (Sogn Andersen et al. 2013). Increased temperature is thus likely to reinforce the negative effects of decreased light availability on most macroalgae. However, in this study, no significant relationship between hard bottom species composition and temperature was found when accounting for other changes in coastal biogeochemistry. One of the species included in the MSMDI-index, sugar kelp (*Saccharina latissima*) has been drastically reduced along the Norwegian (Moy and Christie 2012) and Swedish (Eriksson et al. 2002) Skagerrak coast, where kelp forests have been replaced by filamentous ephemeral algae on rocky-bottom substrates. This is part of a global shift (Filbee-Dexter and Wernberg 2018), which for the North Sea and Skagerrak has been attributed to effects of high summer temperatures, as well as aggregated factors related to particle load, sedimentation and high growth of opportunistic algae and epibionts (Norderhaug et al. 2015; Sogn Andersen et al. 2011). A recent study showed that coastal darkening (due to increased turbidity) significantly reduced kelp productivity and carbon fixation in a coastal system in New Zealand (Blain et al. 2021).

There was also an overall shift in the community structure for the hard-bottom communities, with an increase in the number and abundances of faunal species and a decrease in macroalgal species over time. This has also been shown for the larger Skagerrak area, and was attributed to increased substrate availability, mainly due to reductions in lower growth depth and the density of macroalgae in Skagerrak (Moy et al. 2017). Further, nutrient rich particulate loadings may serve as food for filter feeders, possibly explaining the increased presence of faunal species in hard-bottom communities (Fagerli et al. 2020). These suggestions are also supported by our analyses, pointing to coastal darkening (TSM and POC) as an important driver for the long-term changes in community structure.

The soft-bottom communities had marked differences between the shallow and deep stations over time, where the deeper waters showed a significant improvement in ecological status attributed to a reduction in eutrophication (see Section 4.3), while no improvement was found for the shallow soft-bottom fauna. The species diversity indices for the shallow station did not change over the time period, however there was a slight increase in number of individuals and also number of species, which could indicate an increase in the food supply. Trannum et al. (2018) found an increase in species living in shells and tubes for a number of stations along the Skagerrak coast (including BR1 and BT44) until 2010, where several of these species are specialized to feeding on organic matter on the sediment surface and/or from the water masses. For example, there was an increase in the bivalves *Parvicardium minimum*, *Kelliella miliaris*, *Gorbula gibba*, and *Mendicula ferruginosa* and annelids *Pseudopolydora* sp. and *Sosane wahrbergi*, which are species that live as filter feeders and/or surface deposit feeders (Figures A5 and A6, trait information extracted from the database at the Norwegian Institute for Water Research, see Oug et al. 2012). This shift in feeding mode may suggest a change in the food source pointing to more particulate food in the water column and on the sediment surface. This corresponds to similar findings for the hard-bottom communities,

although a more thorough biological trait analyses is needed to validate this response. In line with our findings, Kroncke et al. (2011) recorded a similar increase in small molluscs in the southern North Sea from 1986 to 2000, which was interpreted as a response to increased food supply. Combined with the finding of increased suspended particle concentrations in the water column (at all depth layers), this could suggest that sedimentation and sinking of particulate matter from the surface layer can act as an increasingly important food source for filter-feeders in both soft- and hard-bottom communities with increasing inputs of terrestrial organic matter (e.g. Bartels et al. 2018).

For both the shallow soft-bottom fauna and the hard-bottom communities, detrended correspondence analysis showed that the species composition changed over time, with gradual change in the 1990s, before more rapid changes occurred from around 2000. These long-term changes in the overall benthic community composition were related to both recovery from eutrophication (reduced water column DIN and PO₄) and increased coastal darkening (increased water column TSM and POC), which in turn were found to be significantly related to the increased riverine discharge to Skagerrak.

In this study, several of the variables show rapid change or extreme concentrations in the time period around year 2000, such as the river discharge and transport (especially TOC, TotN, NO₃ and Si), coastal suspended particle concentrations, Secchi depth and shallow sediment TOC concentrations, in addition to the main ordination axis for the hard-bottom and shallow soft-bottom communities. Several studies report large-scale changes in the Skagerrak around this time period, for example thresholds in particulate concentrations (Frigstad et al. 2013), drastic reduction in sugar kelp forests (Moy and Christie 2012), changes in the phytoplankton and zooplankton communities (Anonymous 2012), as well as poor recruitment of several fish species (Johannessen et al. 2012). In year 2000, there was a large flood yielding exceptionally high riverine discharge and element transports to Skagerrak coastal waters (Kaste et al., 2018),

and this large influx of suspended organic material could have had an impact on the observed shift seen in the nearshore pelagic and benthic communities. However, there was a regime shift reported for the late 1990's for the Northeastern Atlantic and North Sea (Reid et al. 2001; Weijerman et al. 2005; Hatun et al. 2009), connected to large scale changes in circulation patterns and inflow of Atlantic water. The presence of a potential regime shift in Skagerrak coastal waters in the early 2000's and the relative influence of changes in riverine transports, temperature, eutrophication and more large-scale circulation patterns remains to be resolved and should be investigated in future studies.

4.3. Long-term reductions in coastal eutrophication and the need for adaptive monitoring and management

The largest downward trends (between 27-36%) for the coastal biogeochemical variables over the 1990-2016 time period were for the concentrations of DIN and PO₄ for all depth layers. Previous analyses of the contribution of inorganic nutrients of various advected water masses to Skagerrak coastal waters (Aure et al. 1998; Frigstad et al. 2013), have shown that it is particularly reductions in nutrients advected from the German Bight and the southern North Sea that contributes to this long-term nutrient reduction. Also, the concentrations of inorganic nutrients in Norwegian rivers have declined over the last 25 years, especially nitrogen, due to reduced atmospheric deposition (Deininger et al. 2020).

There is an overall decrease in inorganic nutrient loadings and eutrophication status reported for many regions of the North and Baltic Seas (termed oligotrophication; Nixon 1995), which is linked to management efforts to reduce eutrophication (Carstensen et al. 2006; Lundsør et al. 2020; Norderhaug et al. 2016; Vermaat et al. 2008). In this study, we found no significant changes in the annual Chl_a concentrations over time. However, there was a general improvement in ecological status in soft-bottom fauna in deeper, off-shore waters which was connected to a recovery from eutrophication, indicated by an increase in WFD-index (NQI1)

and species diversity (H') over time, as well as an increase in coastal darkening. Trannum et al. (2018) came to the same conclusion based on the time period from 1990-2010, which now is evident also for the entire time series (1990-2016). In line with this observation, tolerant species decreased over time at the deep station (e.g. the small opportunistic annelids *Heteromastus filiformis* and *Notomastus latericeus* and the carnivore annelid *Goniada maculate*), while more sensitive species like tube-building annelids (e.g. the maldanides *Rhodine loveni* and *Euclymeninae indet.* and the terebellomorph annelid *Terebellides stroemi*) increased (Frigstad et al. 2018). The findings in this study point to that increasing riverine runoff due to climate change has counteracted the overall positive effect of oligotrophication in shallower coastal waters, and contributed to a worsening in ecological status for hard- and shallow soft-bottom communities over time (McQuatters-Gollop et al. 2009; Rabalais et al. 2009; Trannum et al. 2018). Increased inputs of terrestrial organic matter from rivers to coastal regions can hinder ecosystem recovery from eutrophication, due to the effects on coastal light availability, flocculation and sedimentation and potential bioavailability for autotrophic and heterotrophic processes (Andersson et al. 2013; Deininger and Frigstad 2019).

Duarte et al. (2009) has described this failure to return to reference status following nutrient reductions for several coastal areas around the globe. This failure is proposed to be a result of the cumulative effects of multiple changes in environmental conditions and interactions over the time period, leading to the 'shifting baseline syndrome' which several coastal areas have suffered from (Dayton et al. 1998; Pauly 1995). Importantly, this has implications for the adaptive monitoring of coastal systems, because effects of ongoing climate change and/or natural variability will act on the ecosystems simultaneously and may mask potential positive effects of reductions in inorganic nutrient loadings. These changes point to implementing adaptive monitoring, where the monitoring program evolves iteratively as the major drivers change, and new information emerges.

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Journal Pre-proof

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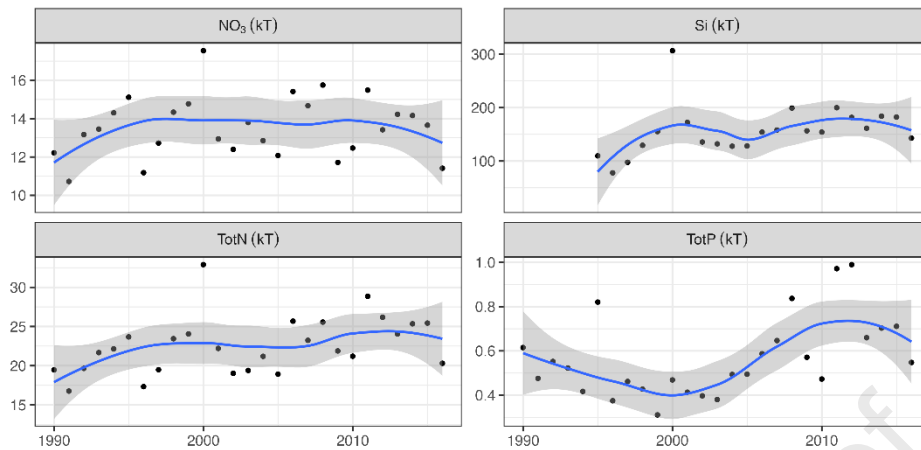
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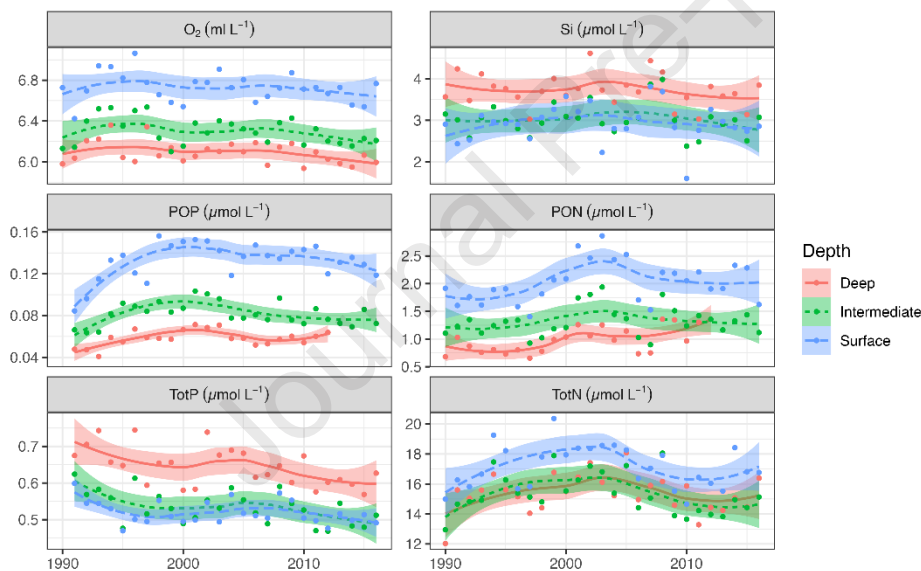
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822 Appendix. Additional figures and tables.



823

824 **Figure A1.** Time series of river transport of NO₃, Si, TotN, and TotP.



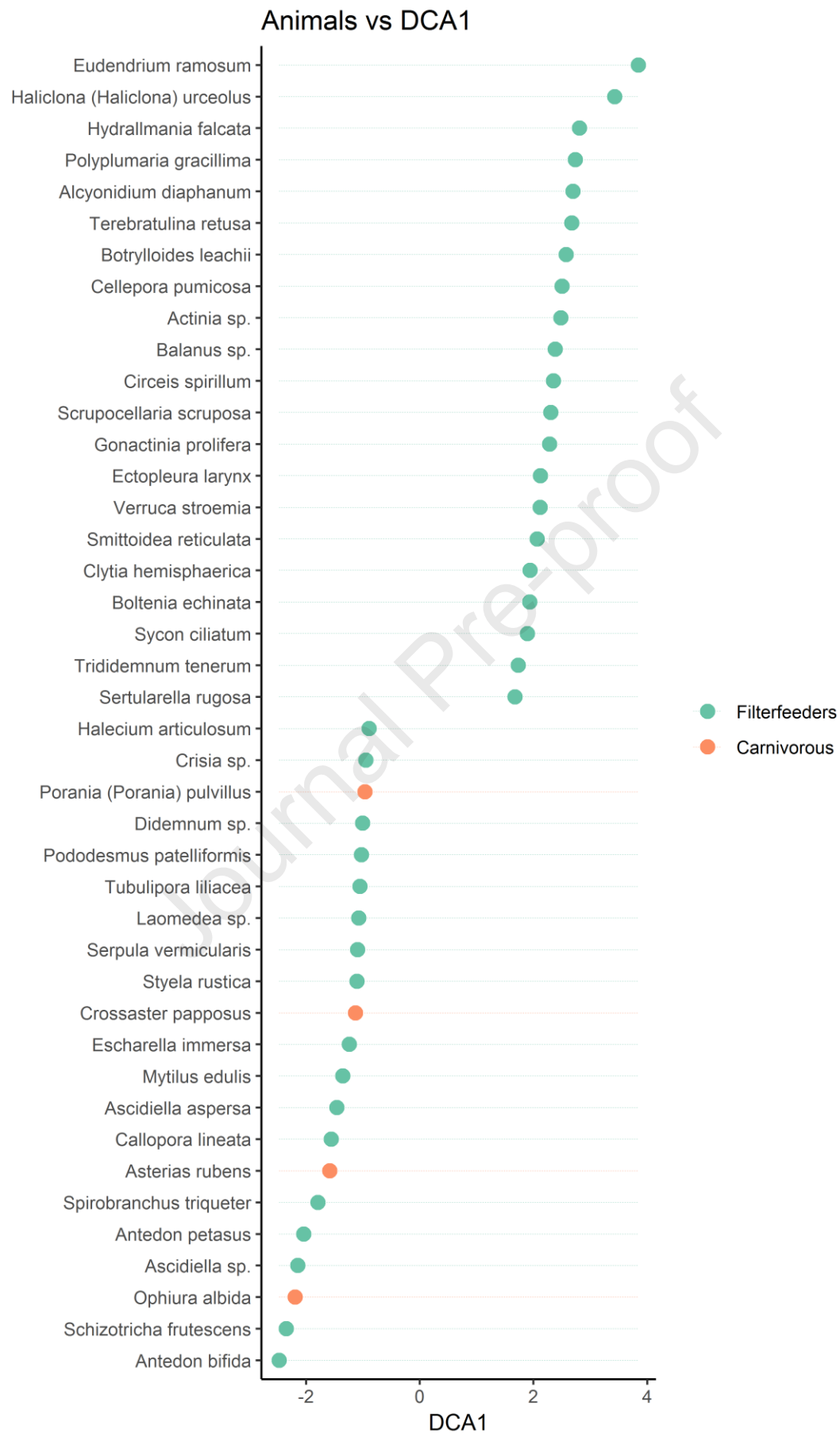
825

826 **Figure A2.** Time series of O₂, Si, POP, PON, TotP and TotN for surface (0-10m),
827 intermediate (20-30m) and deep (50-75m) depth layers at the Arendal station (VT5).



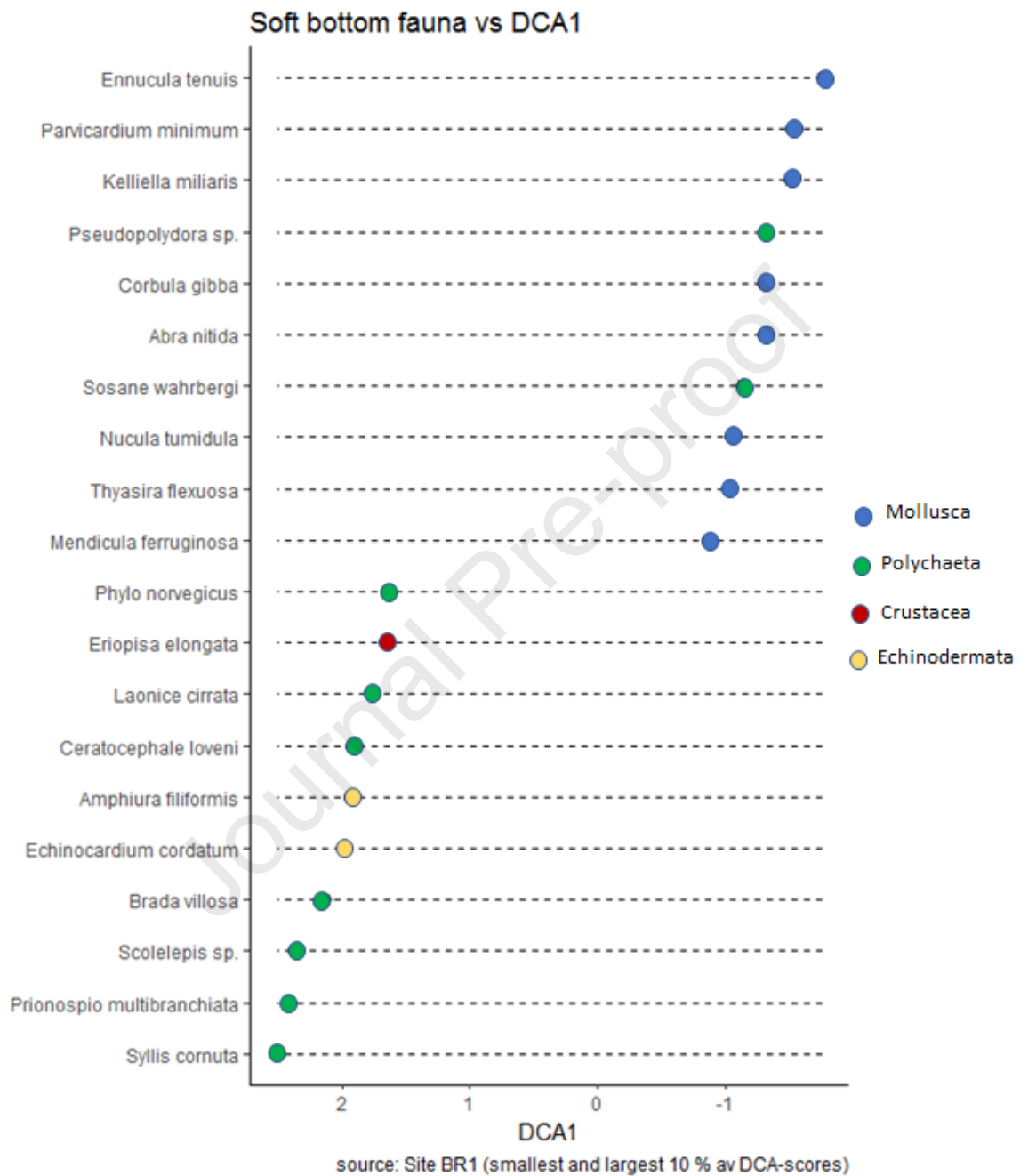
source: Macroalgae subset (smallest and largest 10 % of DCA-scores)

829 **Figure A3.** Species scores obtained from DCA for macroalgae species at hard-bottom
830 stations versus DCA1.



source: Animal subset (smallest and largest 10 % of DCA-scores)

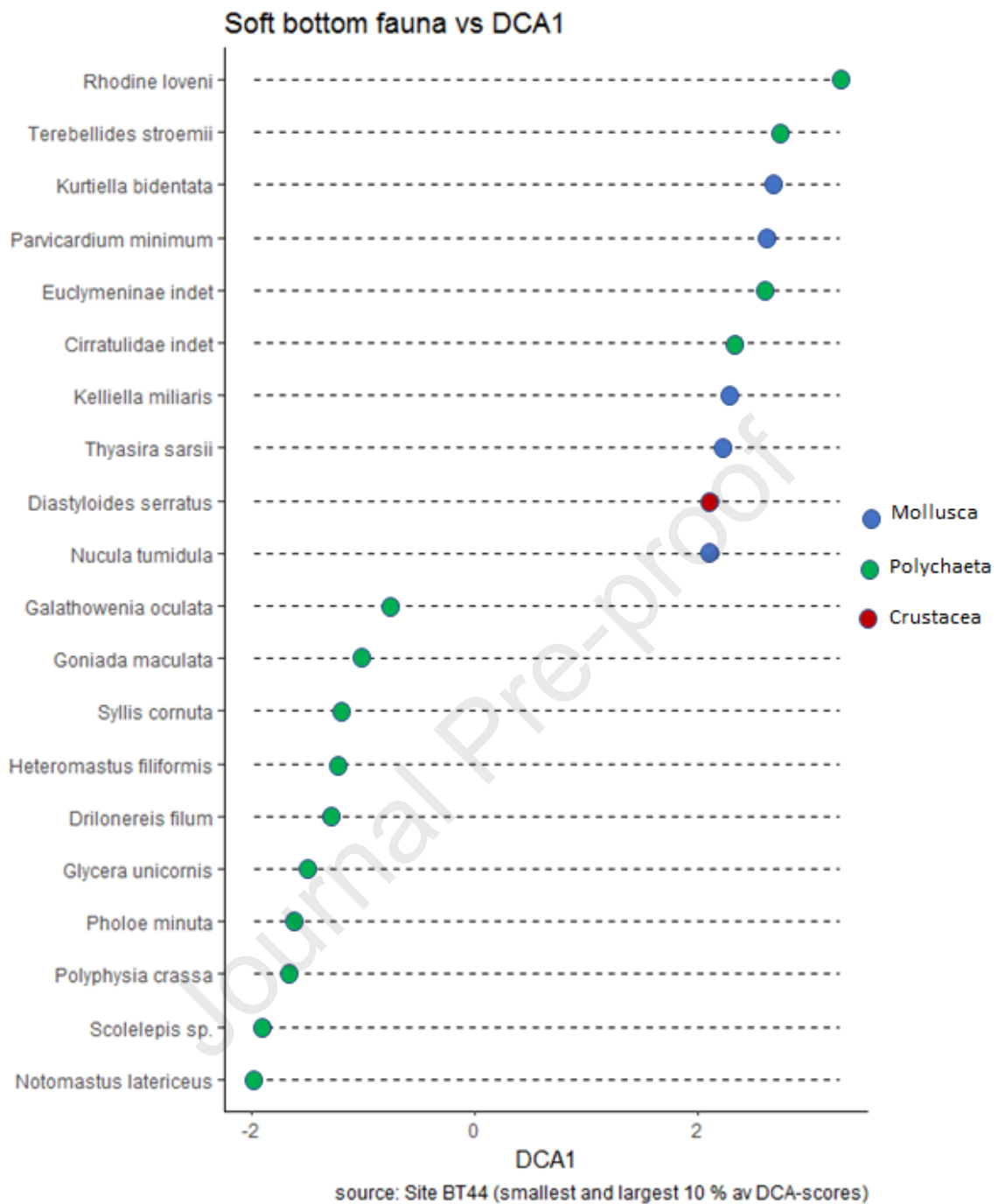
832 **Figure A4.** Species scores obtained from DCA for animal species at hard-bottom stations
 833 versus DCA1.



834

835 **Figure A5.** Species scores obtained from DCA for soft-bottom fauna versus DCA1 for the
 836 shallow station (BR1).

837



838

839 **Figure A6.** Species scores obtained from DCA for soft-bottom fauna versus DCA1 for the
 840 deep station (BT44).

841

842 **Table A1.** Table of time trends of annually aggregated data for all variables in the coastal
 843 biogeochemistry, phytoplankton and river datasets, as well as the MSMDI-index for
 844 macroalgae and Norwegian Quality Index (NQI1) for soft bottom fauna (see Figure 2).

845

Variable	Change per year	Percent change per year	P- value
River_Discharge	429.7	0.90	0.011
River_NO3	33.63	0.25	0.53
River_PO4	7.694	3.30	0.0035
River_Si	3347	2.16	0.008
River_SPM	5849	2.00	0.1
River_TOC	1881	1.04	0.038
River_TotN	199.7	0.90	0.02
River_TotP	9.103	1.74	0.022
Hydro_Chla_Deep	-0.001048	-0.27	0.74
Hydro_Chla_Intermediate	-0.009473	-1.10	0.05
Hydro_Chla_Surface	-0.01144	-0.68	0.23

Hydro_DIN_Deep	-0.08121	-1.41	0.013
Hydro_DIN_Intermediate	-0.0509	-1.10	0.0027
Hydro_DIN_Surface	-0.04959	-1.43	0.0027
Hydro_O2_Deep	-0.004005	-0.07	0.13
Hydro_O2_Intermediate	-0.006723	-0.11	0.2
Hydro_O2_Surface	-0.004992	-0.07	0.21
Hydro_PO4_Deep	-0.004692	-1.08	<0.001
Hydro_PO4_Intermediate	-0.00307	-1.04	0.0031
Hydro_PO4_Surface	-0.00133	-0.60	0.058
Hydro_POC_Deep	0.2299	2.94	<0.001
Hydro_POC_Intermediate	0.1067	1.13	0.004
Hydro_POC_Surface	0.196	1.25	0.0031
Hydro_PON_Deep	0.02417	2.47	0.0051
Hydro_PON_Intermediate	0.005212	0.39	0.32
Hydro_PON_Surface	0.01479	0.77	0.12
Hydro_POP_Deep	0.0003246	0.56	0.28
Hydro_POP_Intermediate	-0.0003997	-0.49	0.4
Hydro_POP_Surface	0.0002597	0.19	0.72
Hydro_Salinity_Deep	-0.002855	-0.01	0.32

Hydro_Salinity_Intermediate	-0.01134	-0.03	0.12
Hydro_Salinity_Surface	-0.03101	-0.11	0.037
Hydro_Secchi_Surface	0.01003	0.13	0.85
Hydro_Si_Deep	-0.007894	-0.21	0.43
Hydro_Si_Intermediate	-0.002968	-0.10	0.68
Hydro_Si_Surface	0.002418	0.08	0.93
Hydro_Temperature_Deep	0.03856	0.44	0.0052
Hydro_Temperature_Intermediate	0.03822	0.40	0.017
Hydro_Temperature_Surface	0.0221	0.22	0.087
Hydro_TotN_Deep	-0.01429	-0.09	0.74
Hydro_TotN_Intermediate	-0.02893	-0.19	0.42
Hydro_TotN_Surface	-0.01162	-0.07	0.9
Hydro_TotP_Deep	-0.003718	-0.57	0.0072
Hydro_TotP_Intermediate	-0.003199	-0.60	0.0082
Hydro_TotP_Surface	-0.001271	-0.25	0.22
Hydro_TSM_Deep	0.01893	2.10	<0.001
Hydro_TSM_Intermediate	0.01102	1.44	<0.001
Hydro_TSM_Surface	0.01581	1.74	<0.001
Plankton_Diatoms	3198	0.95	0.75

Plankton_Dinoflagellates	-5522	-7.79	<0.001
Plankton_Flagellates	-1.154e+05	-4.42	0.015
Hardbottom_Lowergrowth_HR104	-0.003846	-0.43	0.0043
Hardbottom_Lowergrowth_HT113	-0.002308	-0.25	0.04
SoftBottom_NQI1_BT44	8.72e-09	0.006	0.9958
SoftBottom_NQI1_BR1	0.4043506	0.00075	0.10

846

Highlights

- Riverine discharge and transport increased from 1990 to 2016
- Corresponding long-term increase in suspended and particulate organic matter in receiving coastal waters
- Worsening in ecological status of hard-bottom communities and deep soft-bottom fauna attributed to increased riverine loadings
- Shows how climate change can intensify land-ocean interactions and have implications on the potential to achieve good environmental status of coastal waters

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: