# Phytoplankton community dynamics in the Oslofjorden based on a century long time series

*Series of dissertations submitted to the*
*Faculty of Mathematics and Natural Sciences, University of Oslo*
*No. 2466*

ISSN 1501-7710

Cover: Hanne Baadsgaard Utigard.
Print production: Reprosentralen, University of Oslo.

## ACKNOWLEDGEMENT

This PhD has been a long journey. My interest in marine biology started on a school ship in 1993. I am sincerely grateful to each and every one of the crew who have made significant contributions. Firstly, my main supervisor Bente Edvardsen who took me on board at UiO in 2016. You have guided me through these years of work and development with kindness and expertise. Your excellent choice of co-supervisors, Leif Christian Stige and Wenche Eikrem have patiently educated me in statistics and taxonomy, and both of you have reduced my stress by solving problems before they got too big. A big thank to all colleges at AQUA who I have missed this last year, especially the lunches. I am grateful to Svanhild, Toril, Knut and the other members of Fagrådet for support and for sharing their enthusiasm for studying the marine environment in the fjord. To Sindre and the others at F/F Trygve Braarud, thank you for so many happy hours at sea. And to Guri, André and Anette at NIVA, without you, there may not have been a PhD at all.

This project would not have been realised without the support from Norconsult and my former leader Ann-Kristin Vikhagen; thank you for believing in me. There have been some rough seas along the way and Anne Marie and Tom, thank you so much for being there then and smoothly navigating us into calmer waters. The old “marine team” in Horten and the new marine crew and other colleagues in Norconsult, thank you for cheering and putting up with my chaos for so long. My friends, thank you for being there, letting me know that you believe in me and that you love me anyway.

The affection and dedication to the sea was a big part of my childhood, and I must thank my family for starting and following me through on this trip. To my husband Mohammed, Nuru and Nadia, you have secured a happy life and a safe harbour outside the PhD bubble. Together we have successfully managed this and several other challenges these last 5-6 years. Now a new journey will begin.

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# SUMMARY

Phytoplankton are the principal primary producer in the oceans and coastal waters and are essential for producing available organic matter for the following trophic levels of the food chain. On a global scale, the production is high in the temperate waters of northern Europe due to efficient nutrient input and recycling.

However, when the nutrient inputs are too high, as they have been in Oslofjorden for the last century, it has resulted in extreme phytoplankton blooms, like the extensive *Emiliania* blooms that have happened more or less regularly during the previous century. The production of biological material has, together with the release of other organic material from sewage and rivers, exceeded the removal capacity of the bottom communities, resulting in permanent or seasonal hypoxia. The bathymetry of the inner Oslofjorden is a constraint to efficient deep-water renewal and the fjord is therefore especially vulnerable. However, in preindustrial times, the bottom communities had a good environmental status.

The environmental status of the pelagic waters of inner Oslofjorden has improved significantly during the last 50 years. With the implementation of sewage cleaning technology, the ecological condition of the upper water column has improved. A long time series of phytoplankton data with related environmental data was compiled in this project and made it possible to study the long-term effects of the increase and subsequently the reduction in nutrient supply. We found that phytoplankton abundances increased with eutrophication during the first part of the time series. Then a decrease in phytoplankton abundance followed the decline in nutrient releases. Despite the changes in nutrient input, the phytoplankton community's phenology and composition have remained rather constant over the last century. However, the blooms' levels and timing have changed, especially the spring blooms. *Skeletonema* is one of the key taxa in explaining the changes, and increased SST during winter and spring may be one important driver for this change. In the outer Oslofjorden, we find a similar reduction in the spring bloom amplitude, despite minor changes in the levels of nutrients. With global warming, it is predicted by IPCC that the net primary productivity of phytoplankton will “very likely” decline by 2081–2100, relative to 2006–2015 due to increased temperature and stratification, changes in light and nutrient availability, and increased predation.

We hope the compilation of this long-term dataset on phytoplankton and environmental factors will facilitate more research in the future. We have found a correlation between increased temperature and changes in blooming patterns but have not yet succeeded in fully understood the mechanisms that control these changes. Further, we want to study the implication of stratification and possibly changes in the composition of phytoplankton species during the spring bloom. We should also connect to more data and expertise in zooplankton and fish to understand these changes' implications for the food web. The results should ultimately be used in the management of the marine environment.

## LIST OF PAPERS

This thesis is based on the following four papers which will be referred to in the text by their Roman numerals.

I. Lundsør, E., Rigmor, E., Johnsen, M., Engesmo, A., King, A.L., Norli, M., Magnusson, J., Edvardsen, B., Eikrem, W., 2021. Marine phytoplankton community data and corresponding environmental properties from eastern Norway, 1896-2020. Submitted to Scientific Data.

II. Lundsør, E., Stige, L.C., Sørensen, K., Edvardsen, B., 2020. Long-term coastal monitoring data show nutrient-driven reduction in chlorophyll. J. Sea Res. 164, 101925. https://doi.org/10.1016/j.seares.2020.101925

III. Lundsør, E., Stige, L.C., Eikrem, W., M., Engesmo, S. Gran, B. Edvardsen, 2021. Changes in phytoplankton community structure over a century in relation to environmental factors - a long time series.
Submitted to Journal of Plankton Research.

IV. Lundsør, E. and L.J. Naustvoll
Phytoplankton community changes during the spring bloom in Oslofjorden
Manuscript

# INTRODUCTION

The term “plankton” embraces all organisms living wholly or partly in sea or freshwater that drift with the currents and do not have considerable horizontal motility, ranging from viruses to large jellyfish. “Phytoplankton” generally includes the photosynthetic, mostly single-celled microorganisms in this group (Reynolds, 2006a). Approximately half of all the organic production in the world comes from the ocean (Field et al., 1998). Phytoplankton are the principal primary producer in the oceans and coastal waters and produce organic matter available for the following trophic levels of the food chain (Chassot et al., 2010). Phytoplankton growth is primarily controlled by solar light and nutrient availability (bottom-up control). The abundance and structure of the phytoplankton community is controlled by the balance between production and the loss processes such as grazing (top-down control) and sinking (Behrenfeld 2014) (Figure 1). Phytoplankton has an essential ecological function as a primary producer that directly and indirectly fuels food webs. Additionally, it can significantly impact water quality by affecting turbidity and dissolved oxygen concentration, and sinking cells can contribute to oxygen deficiency on the seafloor (Los and Wijsman, 2007). Therefore, changes in phytoplankton abundance, distribution and biodiversity will impact the functions that they play in the natural ecosystem and the human environment.

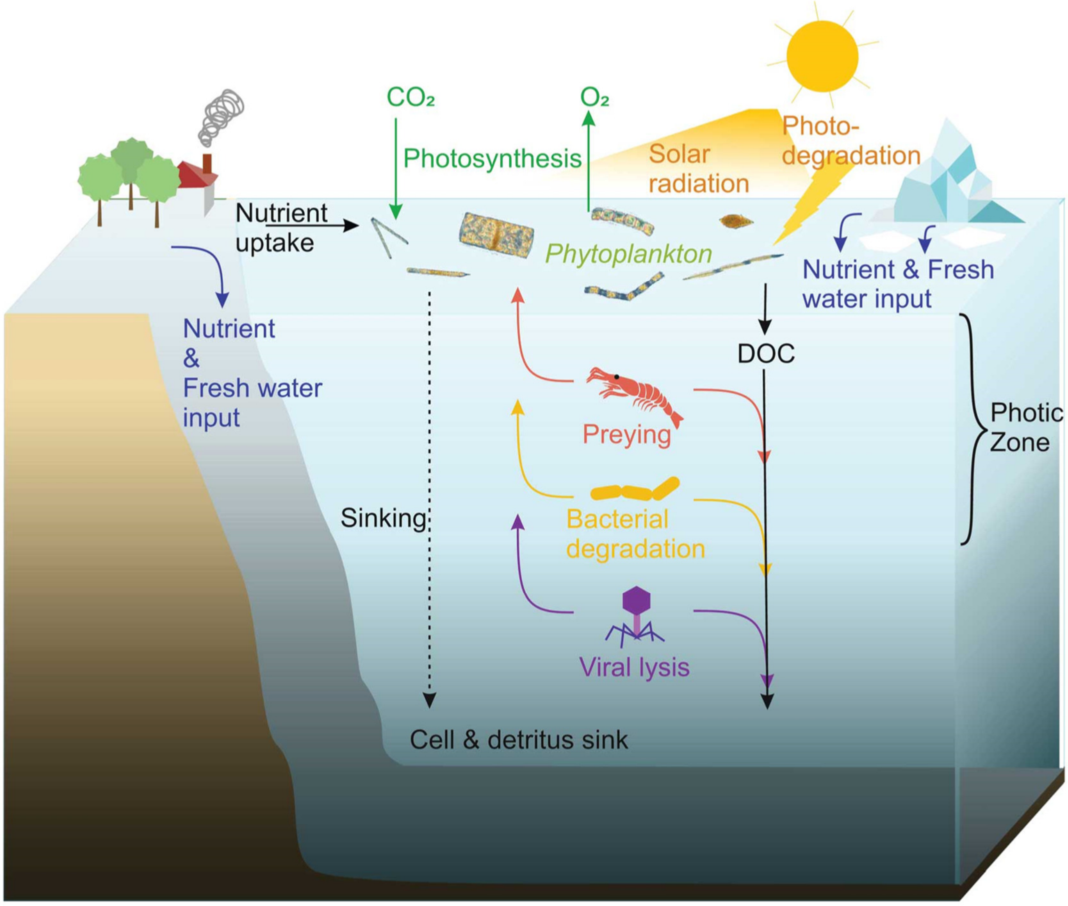


*Figure 1: Cycling of marine phytoplankton. Phytoplankton growth is primarily controlled by solar light and nutrient availability (top-down processes) and by predation and degradation by bacteria or viruses (bottom-up processes). Nutrients and freshwater are released from rivers and population (sewage). Phytoplankton are the principal primary producer in the oceans and serves as prey for zooplankton, fish larvae and other heterotrophic organisms. They also provide dissolved organic carbon (DOC) to the water. Ultimately they will slowly sink to the seafloor.* (Käse and Geuer, 2018)

## Marine phytoplankton distribution and seasonality

### *Global distribution*

Globally, primary production is high in temperate zones. The presence of distinct seasons and upwelling cause mixing of water masses and short-term environmental variability in abiotic factors and nutrients  (Longhurst, 1995). More stable water masses and low nutrient supply over the oligotrophic subtropical gyres of the Pacific and Atlantic oceans results in low primary production here (Behrenfeld et al., 2005) (Figure 2). Turbulence, stratification, wind stress and high nutrient levels will support generalist species with broad niches and reduce richness in temperate zones. Such variability promotes phytoplankton blooms dominated by few species that outcompete and monopolise resources (Righetti et al., 2019). Therefore, fast-growing opportunistic phytoplankton dominates the seasonal blooms at high latitudes (Barton et al., 2020). The more stable environments closer to the equator support high species richness, and there is an evident latitudinal decline in species richness towards the poles (Ibarbalz et al., 2019).

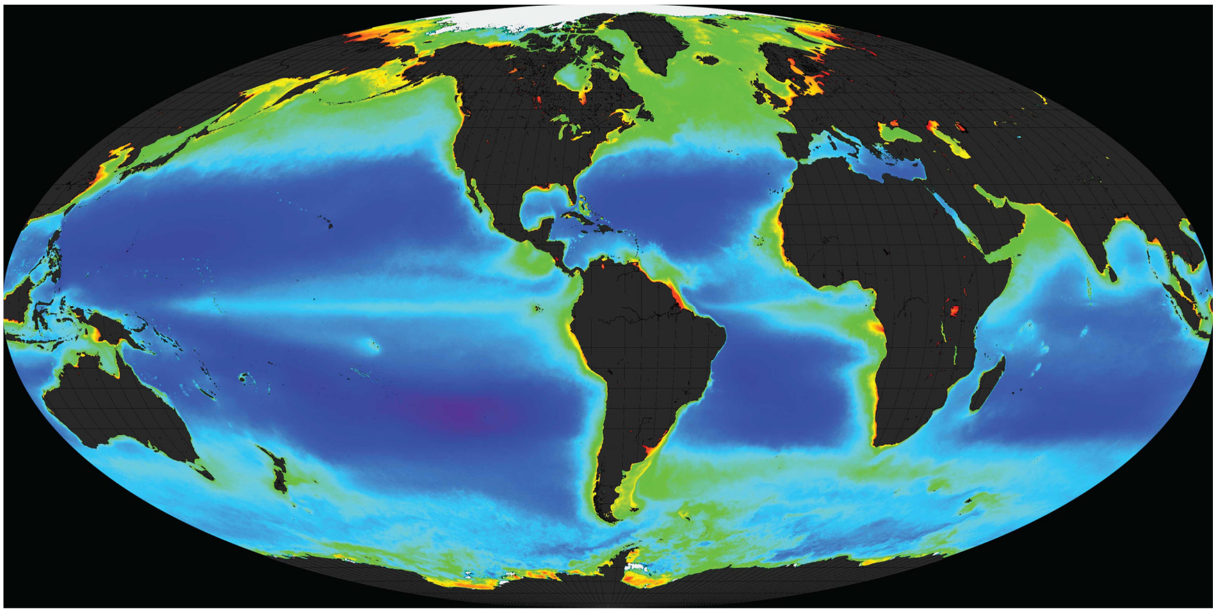


*Figure 2: Global distribution of chlorophyll a. Image courtesy SeaWiFS Project. https://earthobservatory.nasa.gov/images/4097/global-chlorophyll*

Although there are regional variations (McQuatters-Gollop et al., 2007), there is evidence of a global decrease in marine phytoplankton biomass of approximately 1% of the median per year over the past century. One study concluded that global phytoplankton production had declined in 8 out of 10 areas investigated, concurrent with an observed increase in sea surface temperature (SST). In only two areas, the southern Indian Ocean and the Southern Ocean, had phytoplankton biomass shifted from decreasing to increasing in more recent years (Boyce et al., 2010). In contrast, data from the Continuous Plankton Recorder (CPR) surveys showed an increase in chlorophyll concentrations (Phytoplankton Colour Index) in the highly productive northern Atlantic basins. Also, other long-term time series, including the Hawaii Ocean Time series (HOT8), the Bermuda Atlantic Time Series (BATS) and the California Cooperative

Oceanic Fisheries Investigations (CalCOFI), indicate increased phytoplankton biomass over the past 20–50 years (McQuatters-Gollop et al. 2011).

However, IPCC's climate models predict that net primary productivity will "very likely" decline by 2081–2100, relative to 2006–2015. This change will develop due to increased temperature and stratification, changes in light and nutrients availability and increased predation. However, there are regional variations between low and high latitudes. In the polar regions decreasing sea ice coverage is predicted to lead to increased primary production (IPCC, 2019).

### *Seasonality*

Phytoplankton can respond rapidly to environmental changes (Lekve et al. 2006). Seasonal shifts in light and nutrient levels produce a typical pattern of the abundance of different groups in the phytoplankton community. In Norway and other temperate waters, the phytoplankton community is typically dominated by three major groups: the diatoms, the dinoflagellates, and the haptophytes (Simon et al., 2009). The density of phytoplankton is relatively low during winter when light intensity is low and water masses are unstable. Usually, spring bloom starts when the light influx increases in spring and water masses become more stable (Sverdrup 1953). Diatoms, such as *Skeletonema* sp., *Chaetoceros* spp and *Thalassiosira nordenskioeldii*, often dominate the spring bloom (Kristiansen et al. 2001). When most nutrients are consumed, the water column becomes more stratified, and the phytoplankton are partly consumed by zooplankton in the water column and partly sink to the bottom. (Kristiansen et al. 2001). The biomass is usually low during the summer, but it is possible to have summer blooms after run-off episodes in fjord areas (Erga and Heimdal, 1984). The autumn bloom occurs when increasing vertical mixing (convective cooling and winds) renews the nutrient supply in the euphotic zone before light availability becomes limiting (Findlay et al., 2006; Paasche and Ostergren, 1980). In the inner Oslofjorden, as in other Norwegian fjords, it is also common to have a second bloom in May or June when snow is melting in the highlands and nutrient-rich run-off from land reaches the coast (Paasche and Erga, 1988).

## Drivers of phytoplankton production

On short timescales, weeks or months, access to light and nutrients (bottom-up control) drives primary production. However, tidal mixing, salinity, temperature, and grazing are also significant factors. Sinking and mixing processes are also essential drivers, while river discharge plays a considerable role in less saline areas (Blauw et al., 2018).

Therefore, the abundance and structure of the phytoplankton community result from the balance between production, the loss by grazing (top-down control) and sinking rates (Behrenfeld, 2014).

### *Nutrients*

Phytoplankton, like other algae, take up inorganic nutrients from the surrounding water. Decomposition of organic matter and the metabolism of animals or heterotrophic microorganisms will regenerate used inorganic nutrients back to the sea (biochemical cycle). Four elements, P, N, Fe and Si are often present in limited supply and are therefore of crucial ecological importance.

Natural phosphorous comes in small amounts from weathering of phosphatic minerals (Reynolds, 2006b), but many coastal environments receive anthropogenic phosphorus from sewage, farming and industry. Most bioavailable nitrogen in the Oslofjorden is in the form of dissolved inorganic nitrogen (DIN). Anthropogenic activities, especially agriculture, supply DIN to the environment (Staalstrøm et al., 2021)

The human-induced supply of nutrients may function as a fertiliser and increase phytoplankton growth and division very quickly. The primary source of phosphorus in Oslofjord is human activities, with sewage as the significant contributor. In the outer Oslofjorden, agriculture is also a considerable contributor (Selvik and Høgåsen, 2018).

Iron is a micronutrient, essential but required in minimal amounts and rarely problematic except in the large oceans (Reynolds, 2006b).

Silica plays a regulatory role in plankton. It is not a conventional nutrient but is a vital skeletal requirement of diatoms. The amounts of silicon deposited in the cell wall vary both between species and with size (Reynolds, 2006b). Silica concentrations in Oslofjorden vary depending on the season (Paasche and Ostergren, 1980).

Whether primary production by phytoplankton is limited by nitrogen (N) or phosphorus (P) is broadly framed in terms of the relative availabilities of N and P in the water compared to the stoichiometric need for average cell growth, named the Redfield ratio. The Redfield formula: 106C: 16N:1P represents the average composition of a microalgae cell and defines the quantitative relations between the C, N and P biochemical cycles (Redfield, 1958). The Redfield N:P ratio of 16:1 is therefore often used as a benchmark for differentiating N-limitation from P-limitation and is thought to set an upper limit on the nitrate: phosphate ratio in the ocean (Falkowski, 1997; Tyrrell, 1999).

Although the inorganic N:P ratio in the deep sea is remarkably constant and close to 16:1, the plasticity and variability in phytoplankton have been shown many times. The critical N:P is more likely to be in 15-30 (Geider and La Roche, 2002). However, there are considerable variations between species and groups of phytoplankton. Diatoms have lower C:P and N:P ratios than other groups (Ho et al., 2003).

Historically freshwater is considered P-limited (Schindler, 1977) while seawater is considered nitrogen-limited (Ryther and Dunstan, 1971). One critical difference between lakes and estuaries regards the importance of N fixation. Cyanobacteria's ability for N-fixation is one mechanism that leads to P regulation of primary production and eutrophication in freshwater (Schindler, 1977). This N fixation response generally does not occur in estuaries with salinities >10 to 12, even when they are firmly N limited (Howarth, 1988).

The resistance towards recognising nitrogen's importance in estuarine waters has slowed the control of nitrogen pollution (Howarth and Marino, 2010). In the inner Oslofjorden nitrogen removal technology was implemented in the sewage treatment plants from 1997. In the outer

Oslofjorden, there sewage treatment plants still only remove phosphorous. Although there is a higher human population density around the inner parts of Oslofjorden compared to the outer parts, this practice leads to higher levels of nitrogen in the surface waters in the outer Oslofjorden compared to the inner parts (Staalstrøm et al., 2021).

### *Light and temperature*

With light energy, pelagic primary producers reduce carbon dioxide to carbohydrate and oxygen through chlorophyll based photosynthesis (Reynolds, 2006b). It is, however, not a linear relationship between irradiance and primary production. Solar light fluxes vary significantly with the season in the southern part of Norway, from 6 hours daylight during mid-winter to 18 hours daylight in summer. A *Skeletonema* dominating bloom has occurred even in January in Oslofjorden (Dittami et al., 2013), showing enough light for photosynthesis during winter.

Temperature controls the speed of physiological processes and thereby growth and division in phytoplankton. Different taxonomic groups will have different temperature optima. *Skeletonema* is an example of a fast-growing taxon and shows high temperature tolerance and plasticity to salinity and is very common throughout the world, particularly at low temperatures (Carstensen et al., 2015). *Skeletonema* is dominating the spring bloom in Oslofjorden (Paasche and Ostergren, 1980). *Prorocentrum* is more correlated to higher temperatures and is typically a summer-blooming taxon (Horner, 2002).

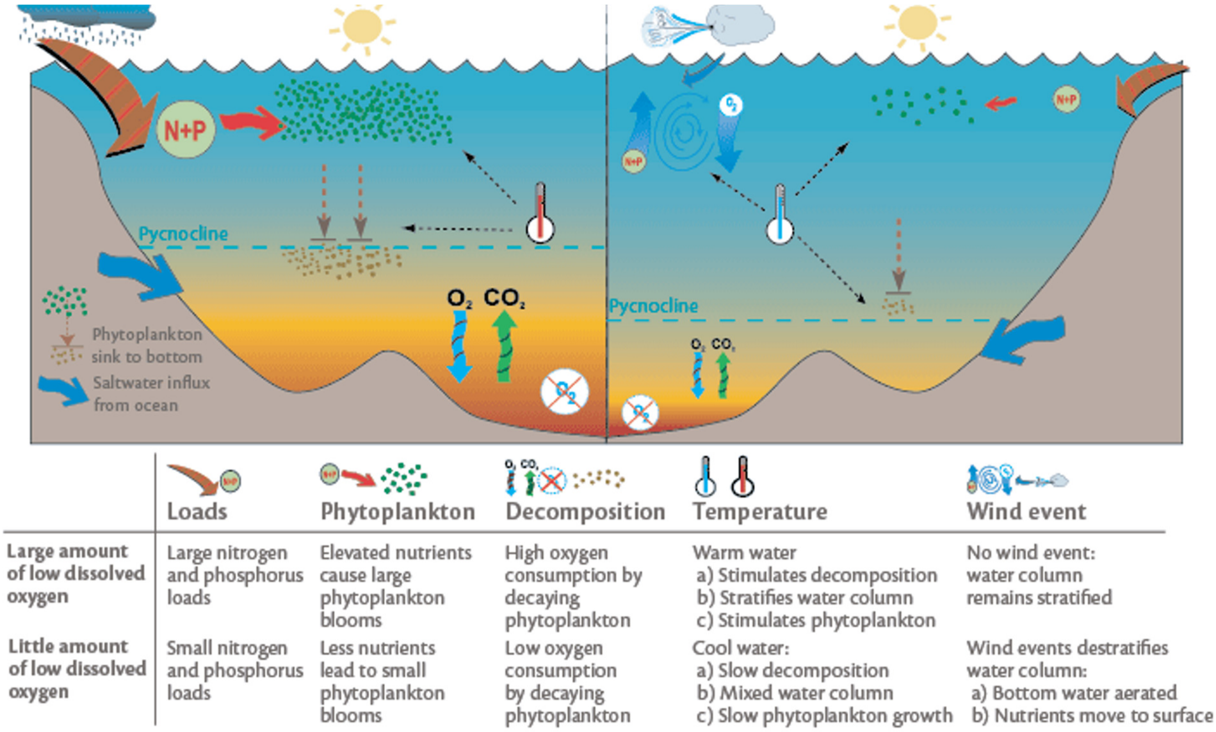
Temperature also has an indirect effect on the pelagic environment by contributing to stratification. Stratification of the water column is a prerequisite for the first annual bloom. Increased stratification permits photosynthetic plankton to keep their vertical distribution in the photic zone. Higher winter temperatures may lead to earlier stratification and decrease the amount of nutrients available for growth (Winder and Sommer, 2012).

An increase of nutrients in the water column will theoretically stimulate increased phytoplankton production. However, despite an increase in nutrients in Oslofjorden, there is a decrease in the levels of chlorophyll (Staalstrøm et al., 2021). Changes in light conditions will possibly reduce phytoplankton growth even under the right nutrient conditions (Frigstad et al. 2020).

## Impact of eutrophication

Eutrophication is a significant threat to coastal marine ecosystems worldwide (Cloern, 2001). Increased supply of nutrients to the ecosystem cause decreased surface water quality (Nixon, 1995; Paasche and Erga, 1987), increased phytoplankton production, and increased risk of toxic algal blooms (Heisler et al., 2008). Sinking plankton biomass contribute to oxygen consumption, thereby lowering oxygen levels in the deeper basins (Cloern, 2001; Staalstrøm, 2015), Figure 3.

The limited water exchange in the Oslofjorden makes the deep basins vulnerable to pollution, especially nutrients and organic matter, which may lead to a high level of oxygen consumption in the deep-water (Staalstrøm 2015). Today, there are several basins in the fjord where the oxygen levels are permanently low. Interestingly, paleoecological analyses have shown that the ecological conditions on the sea bottom in the inner Oslofjorden were good in pre-industrial times. Following the development of bottom-water oxygen deficiency, the environmental condition started to decline in the deeper, inner parts during the late 1800s. During the 1900s, the negative trend developed to shallower depths and broader parts of the fjord (Dolven et al., 2013).



| | Loads | Phytoplankton | Decomposition | Temperature | Wind event |
|---|---|---|---|---|---|
| **Large amount of low dissolved oxygen** | Large nitrogen and phosphorus loads | Elevated nutrients cause large phytoplankton blooms | High oxygen consumption by decaying phytoplankton | Warm water<br>a) Stimulates decomposition<br>b) Stratifies water column<br>c) Stimulates phytoplankton | No wind event: water column remains stratified |
| **Little amount of low dissolved oxygen** | Small nitrogen and phosphorus loads | Less nutrients lead to small phytoplankton blooms | Low oxygen consumption by decaying phytoplankton | Cool water:<br>a) Slow decomposition<br>b) Mixed water column<br>c) Slow phytoplankton growth | Wind events destratifies water column:<br>a) Bottom water aerated<br>b) Nutrients move to surface |

*Figure 3: Conceptual diagram detailing the factors that determine the dissolved oxygen content of a fjord or bay. Diagram courtesy of the Integration and Application Network (ian.umces.edu), University of Maryland, Centre for Environmental Science.*

## Impact of climatic changes/warmer climate

Recent calculations by The Norwegian Meteorological Institute show that the meteorological spring starts about two weeks earlier in the Oslofjorden today compared to 20 years ago (Anon, 2021a). This means that terrestrial growth starts earlier and snow is melting earlier, followed by earlier spring floods in rivers and waterways (Anon, 2021a). These changes affect phytoplankton physiology. Simulation studies have shown increased phytoplankton metabolism with increasing temperature (Taucher and Oschlies, 2011). However, several studies show that rising temperature leads to lower phytoplankton biomass as increased stratification can limit access to nutrients and light (Winder and Sommer, 2012). Higher temperatures may also increase herbivore grazing activity and reduce the phytoplankton biomass (Borkman and Smayda, 2009). Increased stratification and freshening of the upper parts of the water column at higher latitudes such as the Oslofjorden is projected to be a *very likely* consequence of global warming (IPCC, 2019). This increased stratification may prevent vertical mixing of water bodies and thereby access the phytoplankton to access nutrient sources from deeper waters (IPCC, 2019; Winder and Sommer, 2012).

### Chlorophyll *a* as indicators of environmental status

Chlorophyll *a* is commonly used as a proxy for phytoplankton biomass and as an indicator for environmental status of water bodies. It is currently the only biological indicator of ecological status in marine pelagic waters of Norway implemented in the EU Water Framework Directive (WFD, 2000/60/EC). WFD sets out a requirement that water should be of "good" to "very good quality," as measured by ecological measures of quality and rely on our ability to determine the definition of these (Borja et al., 2010). Norway adopted the WFD in 2000, and the Norwegian Environment Agency published the first national guidelines in 2013.

Chlorophyll *a* is assumed to have an approximately linear relationship with the amount of carbon (C) produced (Devlin et al., 2007). There are very similar patterns between the seasonal curves for chlorophyll and phytoplankton biomass and abundance. Still, studies from temperate waters show seasonal variation in the C:Chla *a* values (Jakobsen and Markager, 2016).

There may be several reasons for this. Water analysis of chlorophyll *a* includes small cells and cyanobacteria, which cannot be identified and counted under a light microscope (Bratbak et al., 2011). Additionally, seasonal peaks in chlorophyll *a* may consist of different species with variable pigments throughout the year and the cellular chlorophyll *a* content may vary when irradiance fluctuates (high light adaptation) (Henriksen et al., 2002). *Skeletonema cf. costatum* can reduce the cellular content of chlorophyll *a* with 70% from low to high irradiance (Laviale and Neveux, 2011). However, several uncertainties also influence the calculation of cell volume and carbon content. It is based on microscopic analysis and depends on the quality of the sample age and fixative, equipment and operator (Jakobsen and Markager, 2016).

### Time-series

The value of continuous monitoring and time-series analyses goes beyond understanding the long-term effects of the actual organism or area studied. Together with being the best tool to assess, model and predict the effect of anthropogenic or natural environmental changes, it can also function as a natural laboratory for research about ecological processes which reaches further than the local sampling area (Zingone et al., 2019). A prerequisite for this is that the sampling data is available as a quality assured open-access dataset, which will ensure reproducible analysis and possibilities for further analyses on the same dataset.

In Norway there exists few long-term time series of phytoplankton data. Except for the inner and outer Oslofjorden and the Flødevigen station of the Institute for Marine Research (IMR), the coastal monitoring programmes (Økokyst) are developing time series for phytoplankton and environmental variables from many stations along the Norwegian coast.

In Europe the most well-known phytoplankton long time series are:

- Station MaChiara (MC) – Gulf of Naples, Stazione Zoologica Anton Dohrn, Napoli, Italy (Ribera d 'Alcalà et al., 2004)
- Station L4 – Plymouth, UK, Western Channel Observatory; NERC National Capability of the Plymouth Marine Laboratory and Marine Biological Association (Widdicombe et al., 2010).
- The "Helgoland Roads", Biologische Anstalt Helgoland (BAH) – Alfred Wegner Institute for Polar and Marine Research, Helgoland, Germany (Wiltshire et al., 2010).
- SOMLIT-Astan – French national monitoring station off Roscoff run by CNRS/UMPC, North East English Channel, France (Guilloux et al., 2013).

## Objectives

The overall aim of this thesis was to study the long-term changes in the phytoplankton community in the Oslofjorden in relation to eutrophication and climatic changes.

The first aim was to compile phytoplankton and environmental data from research- and monitoring projects conducted in inner Oslofjorden during the last century.

Secondly, we wanted to use the data collected to understand how chlorophyll-a levels have changed over time and investigate the drivers of these changes. In particular, we wanted to determine how nutrient levels, together with temperature and salinity, control chlorophyll levels through the year (seasonality) and over the years.

Thirdly, we addressed the following questions:

- Has the seasonal pattern of phytoplankton taxonomic composition and abundance changed over time in the inner Oslofjorden?
- Have the phytoplankton taxa that dominate the blooms changed during the last century?
- Has the occurrence of harmful algae changed over time?

Finally, we wanted to compare the results from the inner to the outer part of Oslofjorden and address the consequences of climate change. Specifically, we wanted to investigate if the phytoplankton abundance during spring bloom has changed during the last 20 years and how this relates to abiotic factors such as nutrients, salinity and stratification. In addition, we wished to investigate if the increased riverine inputs of nutrients have led to coastal darkening, which could also potentially explain the decrease in phytoplankton.

# METHODS

## The Oslofjorden study site

The Oslofjorden is Norway's most urban and densely populated coastline, with 1.6 million people (Anon, 2021b). Population growth and densification are expected, with consequences for discharges and surface water. The counties around the Oslofjorden have the country's largest agricultural areas (average 17%, compared to the other counties' average of 3.4%). In addition, the topography of southern Norway means that water from "the whole" of Eastern Norway drains into the Oslofjorden (Moland 2021).

While the inner Oslofjorden is a small sill fjord (190 km$^2$ size), the outer part is an open fjord of 2000 km$^2$ (Baalsrud & Magnusson, 2002) but with several side fjords (Staalstrøm et al., 2021). The two parts are connected through the Drøbaksundet, where the sill is as shallow as 19.5 m. North of the Drøbak sill there are more sills that divide the fjord into several basins, such as Vestfjorden, Bærumsbassenget, Bekkelagsbassenget and Bunnefjorden. This bathymetry is a constraint to efficient deep-water renewal (Magnusson and Berge 2015b; Staalstrøm 2015) that take place in the inner part only on average every 3-5 years (Baalsrud & Magnusson, 2002). In the south, the Oslofjorden is connected to the Skagerrak Sea. There are also many basins in the outer fjord, but only the side fjords are vulnerable to the lack of deep-water removal (Staalstrøm et al., 2021).

The Inner Oslofjorden is a relatively sheltered area with calm weather, warm summers, and cold winters.  Typically, with southern winds in the summer and northerly winds during winter. Longer periods of northerly winds are favorable for water exchange since they pull the surface layer southwards and facilitate the influx of oxygen-rich Atlantic and saline water which flows northwards along the bottom and past the sills. Climatic changes seem to lead to weaker or shorter periods of these northerly winds, impacting the frequency of deep-water exchange (Thaulow and Faafeng 2014).

Rivers, waterways and land run-offs are the key contributors of bioavailable phosphate in the fjord, but the contribution from sewage plants and especially overflow run-off is also significant. However, a major part of the total delivery of organic substances, which contributes to oxygen consumption below 20 meters, is released from the sewage plants (Vogelsang 2011).

Four big rivers that drain eastern Norway (most densely populated part of Norway) are released in the Oslofjorden. Therefore, the outer Oslofjorden is under a continuous and strong anthropogenic influence (e.g. urbanisation and domestic sewage input) that compromise its use and water quality. Recent estimates show that these four rivers contribute to 74% of the total nutrient loads. These loads also enter the inner Oslofjorden and contribute to increasing nutrient levels in the Skagerrak (Staalstrøm et al., 2021).

An increase in eutrophication and release of particles increase the problem of decreased oxygen quality in many deep basins. Together with continuous trawling that disturbs the habitats, these may be the reasons for the observed decrease in demersal fish populations in the Oslofjorden (Moland et al., 2021). At the same time, reductions of the seagrass beds and the kelp forest are also found together with higher abundance of introduced marine species

(Rinde et al., 2021). The management of the Oslofjorden is now a national concern, and a new management plan is in place (Anon, 2021b).

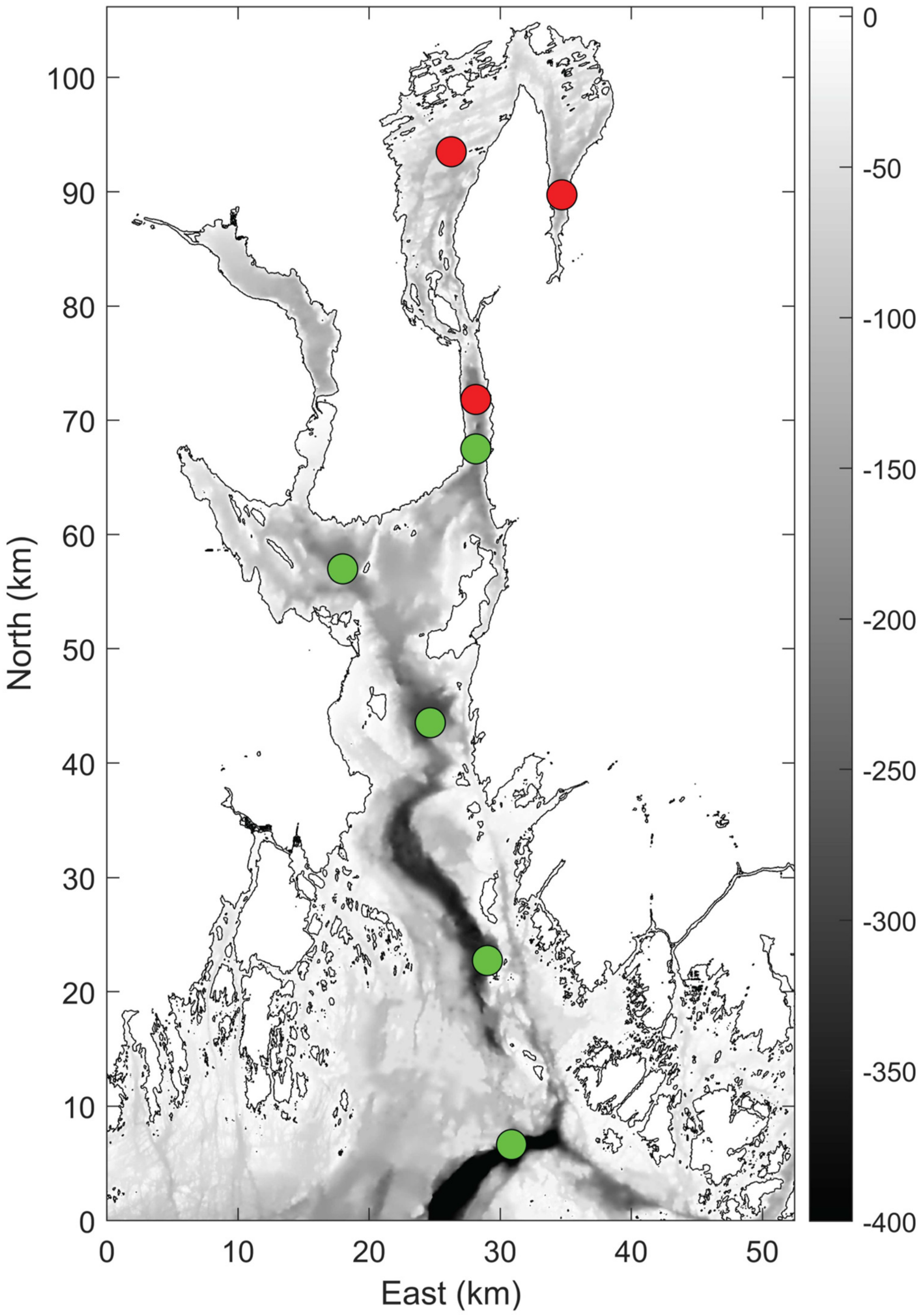


*Figure 4: Study area Oslofjorden. The dots represent the main sampling stations, where red is the inner Oslofjorden and green in the outer Oslofjorden. The greyscale bar depicts the depth in meters.*

## Phytoplankton data compilation

Phytoplankton data from the Oslofjorden have not previously been available in one database. Therefore, during this project, we compiled data from a range of research- and monitoring projects conducted in the Oslofjorden from 1896 until 2020. Historical data from before 1994 was found as handwritten or printed tables in reports and published sources and digitalised. Data from 1994 and onwards have been accessed digitally from the NIVA's databases.

After compilation, the data were checked for digitalisation errors, which could occur during manual digitalisation or just the compilation process. Duplicates and zero values were removed. As the microalgae taxonomy is in constant revision, we have used the original names in our database and matched them to accepted names in the open-access reference system; World Register of Marine Species (Worms) (WoRMS Editorial Board, 2021). We also cross checked the last updated nomenclature in Algaebase (Guiry and Guiry, 2021) to assign species to a valid class name. Before matching the species list, the original species names were cleaned from spelling mistakes, or just spelling mismatches like spaces, commas, etc.

## Time series analysis – General additive modelling (GAM)

The overall question in this thesis is how the phytoplankton community have changed over the century. We want to study if the different variables such as phytoplankton biomass and abundance have changed and how this is controlled by nutrient, salinity and light. In temperate waters, there is a strong seasonal component. The data is collected throughout the year over many years and with different sampling frequencies.

Time series analysis is a technique to derive a trend across time. There are multiple approaches to this and we have chosen General additive modelling (GAM) (Wood, 2017). This is a commonly used method for modelling long time series, especially when the seasonal component is strong. A Generalised Additive Model (GAM) does this by identifying and summing multiple functions that result in a non-linear trend line that best fits the data.

- any trend or long-term change in the level of the time series, and
- any seasonal or within-year variation, and
- any variation or interaction in the trend and seasonal features of the data,

The principle behind GAMs is similar to that of regression, which is a measure of the relation between the mean value of one variable (e.g., biomass of phytoplankton) and corresponding values of other variables (e.g., day of year and years).

GAMs are non-parametric regression models, where the relations between the response variable and the explanatory variables are represented by smooth functions. This means that GAMs do not require predefined mathematical equations describing the presumed relationships because the general shape of these relationships is captured by the smooth functions. GAMs were fitted time series for total phytoplankton and the main phytoplankton groups.

Except that instead of summing effects of individual predictors, GAMs are a sum of smooth functions. In smoothing, the data points of a signal are modified, so individual points higher than the adjacent points (presumably because of noise) are reduced, and points that are lower than the adjacent points are increased, leading to a smoother signal.

Smooth functions allow us to model more complex patterns, and they can be averaged to obtain smoothed curves that are more generalisable.

We considered three models with different levels of complexity. The predictor variables were the day of the year (D) and year (Y). Model M1 included average seasonal patterns with the assumption of no trends between years. Model M2 included trends between years but had the assumption of no changes in seasonal patterns over the years. Model M3 included seasonal and interannual trends and allowed for possible changes in seasonal patterns over the year.

Comparison of the three models (M1-M3) by finding the model with lowest AIC and GCV showed us which model had the best performance. From this we could find out if i.e., overall biomass or chlorophyll *a* levels are dominated by seasonal or annual changes or a combination of both. Overall, we found that the most complex model, M3 performed best for all variables, which implies that both overall levels and the seasonal pattern have changed over time.

## RESULTS

There are a few long-term time series of phytoplankton data in Norway (from Flødevigen by IMR, the monitoring of inner and outer Oslofjorden and from the Økokyst programmes), but they are not publicly available. Therefore, to conduct the analysis for this project, we have compiled a large dataset: "Phytoplankton sampling in the inner part of Oslofjorden" (PAPER I). The dataset is a comprehensive data collection comprising quantitative phytoplankton cell counts and biovolumes with associated metadata, and additional abiotic hydrographical and water chemistry data. The database consists of 605 sampling events resulting in 23,647 phytoplankton taxon records (Figure 5). The primary data source for the collection is the monitoring programme for inner Oslofjorden conducted with varying annual frequencies from 1973 until today, mainly by the Norwegian Institute for water research (NIVA). The database is supplemented with data from various research projects from 1896 to 1965, conducted by researchers from the University of Oslo (UiO). The database can be downloaded from https://doi.org/10.15468/gugesq, and further information about the dataset is described in PAPER I.

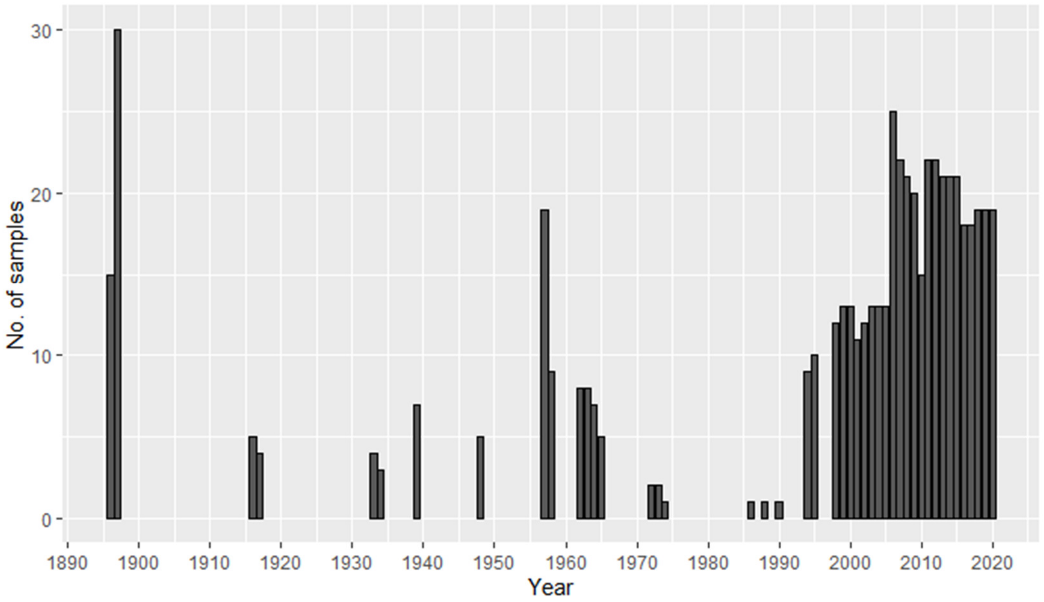


*Figure 5: Number of phytoplankton sampling events per year registered in the Oslofjorden phytoplankton database (PAPER I).*

As the population of Oslo grew, more and more sewage entered the fjord. In the 1960s, the first sewage cleaning plant was put into operation. In 1973 the programme for monitoring the marine environment of the inner Oslofjorden started. In PAPER II, we studied the response of the phytoplankton production to nutrient inputs from 1973 to 2019.

The analysis results in this paper show how levels of chlorophyll *a* have decreased significantly since 1980 (

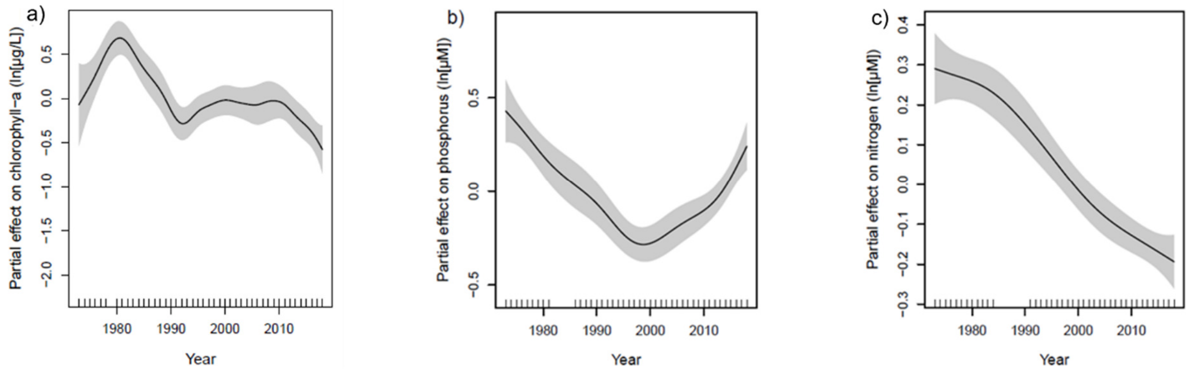


Figure 6). This decrease correlates with a decrease in nitrogen and phosphorus.

For the first 25 years of the time series (1973-1998), phosphorous (P) loads in surface waters decreased as P-reduction technology was gradually introduced (

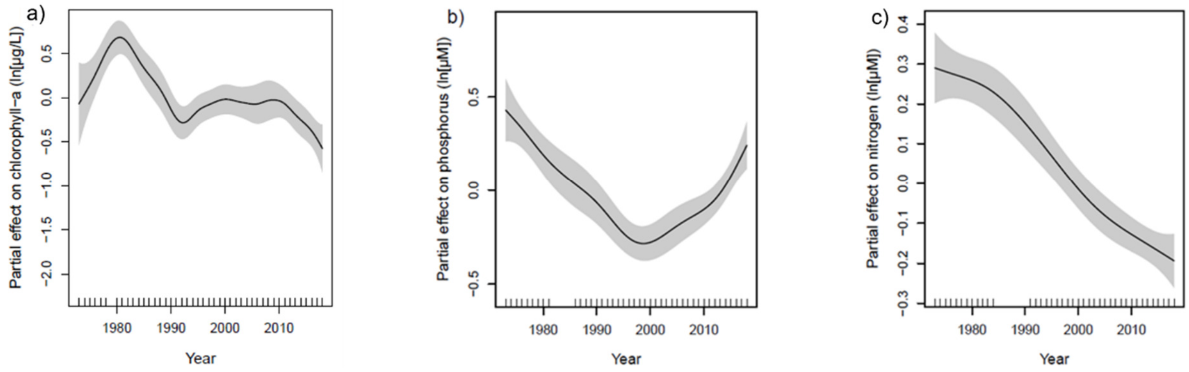


Figure 6). However, after 2000, P loads in surface waters began to increase again. Nitrogen (N) loads have gradually decreased during the whole study period. N-removal technology was introduced to the sewage treatment plants between 1997 and 2000. Despite an increase in human population, the reduction of N loads in the upper water column has continued. Both decreased production of phytoplankton and increased water clarity were related to this. Seasonality of both N and P shows a clear dependency on chlorophyll (

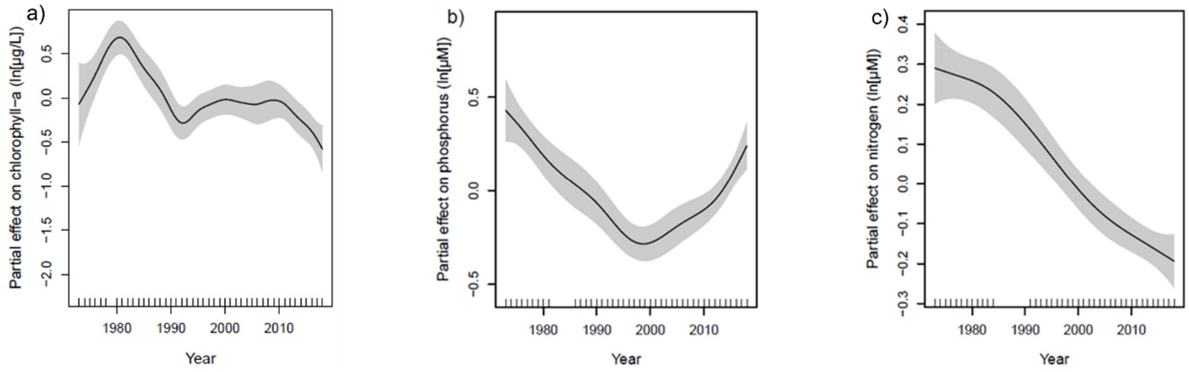


Figure 6). Specifically, we found a positive correlation between chlorophyll *a* and P during spring and chlorophyll *a* and N during autumn. This correlation indicates that P significantly limits growth during the spring bloom and N limits growth during summer and autumn. Since the increase in P levels from the 2000s seems not to have led to increased chlorophyll levels, we suggest that nitrogen may have become more limiting earlier in the season in later years. Although phosphorus levels are rising again, chlorophyll *a* levels are still low. We therefore suggest that this is because nitrogen is limiting the growth. If nitrogen increases again, the chlorophyll *a* level may also begin to rise.

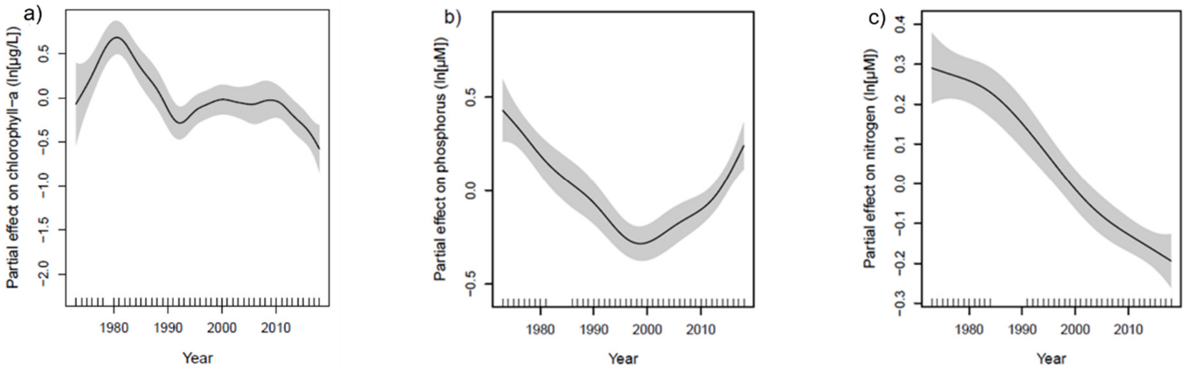


*Figure 6: Yearly changes in chlorophyll a, phosphorus and nitrogen from 1973 to 2017 at DK1 (Steilene) in the inner Oslofjorden. The tick marks on the x-axes in panels a and b and the dots in panel c show the locations of the data. White areas in panel c are due to a lack of data (PAPER II).*

In PAPER III, we have used the data on phytoplankton biomass and abundance to further study the changes in the seasonal pattern of phytoplankton taxonomic composition and abundance during the last century.

Comparison of three GAM models (M1-M3) for 2006–2020 showed that the most complex model, which included seasonal and interannual trends, performed best for all taxonomic groups. This result indicates that both overall biomass levels and the seasonal pattern in biomass have changed since 2006. Predictions derived from this model is shown in Figure 7. The analyses show a general reduction in phytoplankton abundance based on cell counts since the 1970s, especially for the diatoms (Figure 7). The analysis also showed that there had been a change in seasonality towards later spring and autumn blooms, especially since 2013. Our results suggest that this change is mainly driven by diatoms.

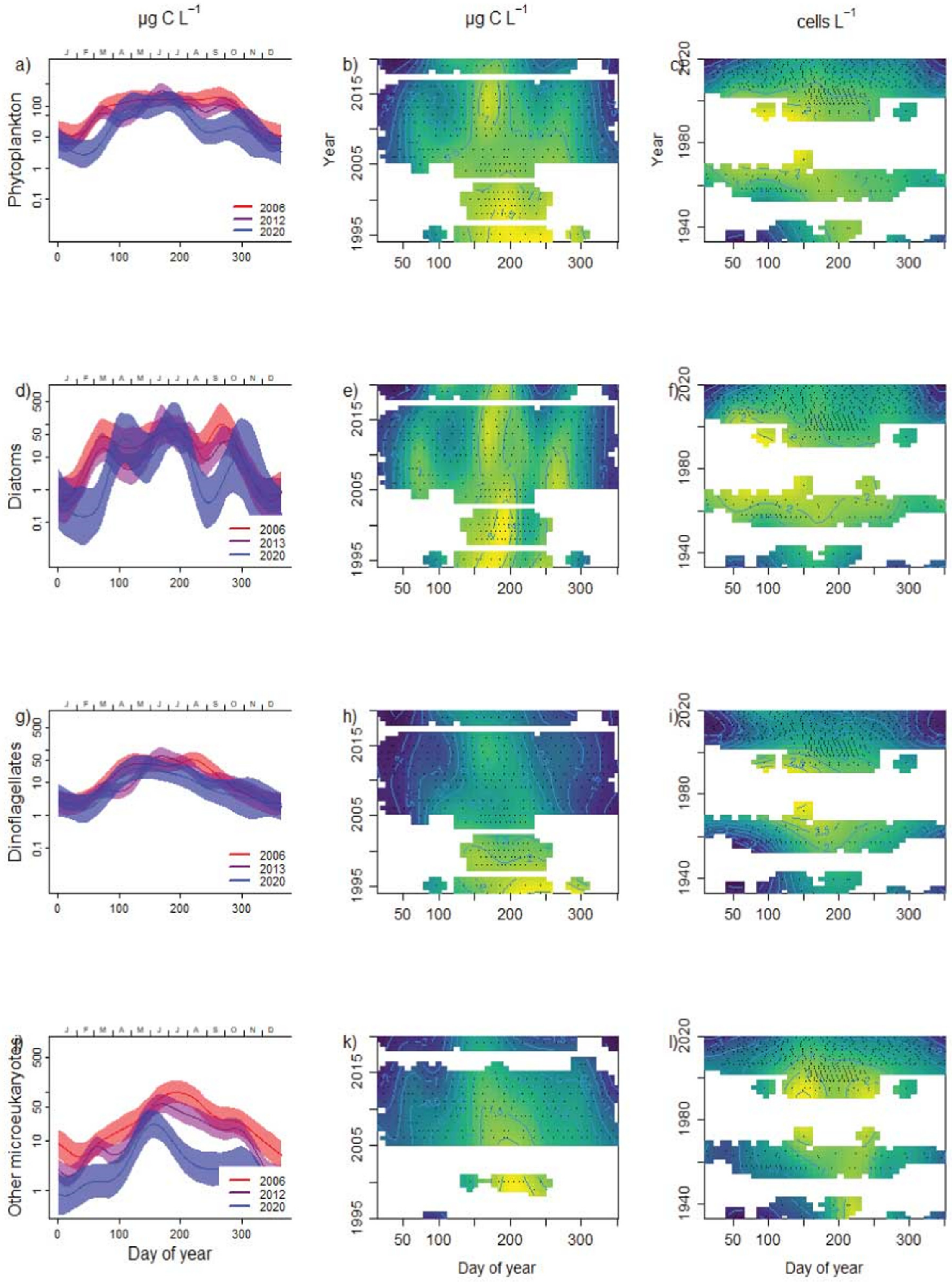


*Figure 7: Seasonal and yearly changes in phytoplankton biomass or abundance at station S1 in the inner Oslofjorden. Left panel: Seasonal patterns in biomass for the period 2006-2020 estimated by model M3. Solid line is the smoothed curve fitted by the GAM-model Eq. 5 and the light-coloured areas represent the 95% confidence bands. Middle panel: Combined seasonal and interannual patterns for biomass in the period 1994-2020. Right panel: abundance for the period 1933 to 2020. Values are shown with lighter colours for higher levels. Dots in middle and right panels show the locations of the data. White areas in middle and right panels are due to lack of data (PAPER III).*

The results indicate a reduction in abundance of key genera of diatoms such as *Skeletonema* and *Chaetoceros*, common during the spring bloom. However, *Pseudo-nitzschia,* common during late spring and early summer, does not show the same decrease.

Further analysis of the drivers of these changes shows a positive interannual correlation between phosphorus and the biomass of all phytoplankton groups are positive both during spring and autumn, which corresponds to the positive correlation found between chlorophyll *a* and phosphorus in Paper II. The positive correlation between nitrogen and chlorophyll *a* corresponds to the positive correlation between nitrogen and dinoflagellates (Figure 8).

There is a correlation between high salinity, low temperature, and high diatom biomass during the first three months (Jan-Mar) of the year (Figure 9). The correlation turns to positive between diatoms and sea surface temperature (SST) during April and May, implying that high SST is associated with a delayed diatom spring bloom.

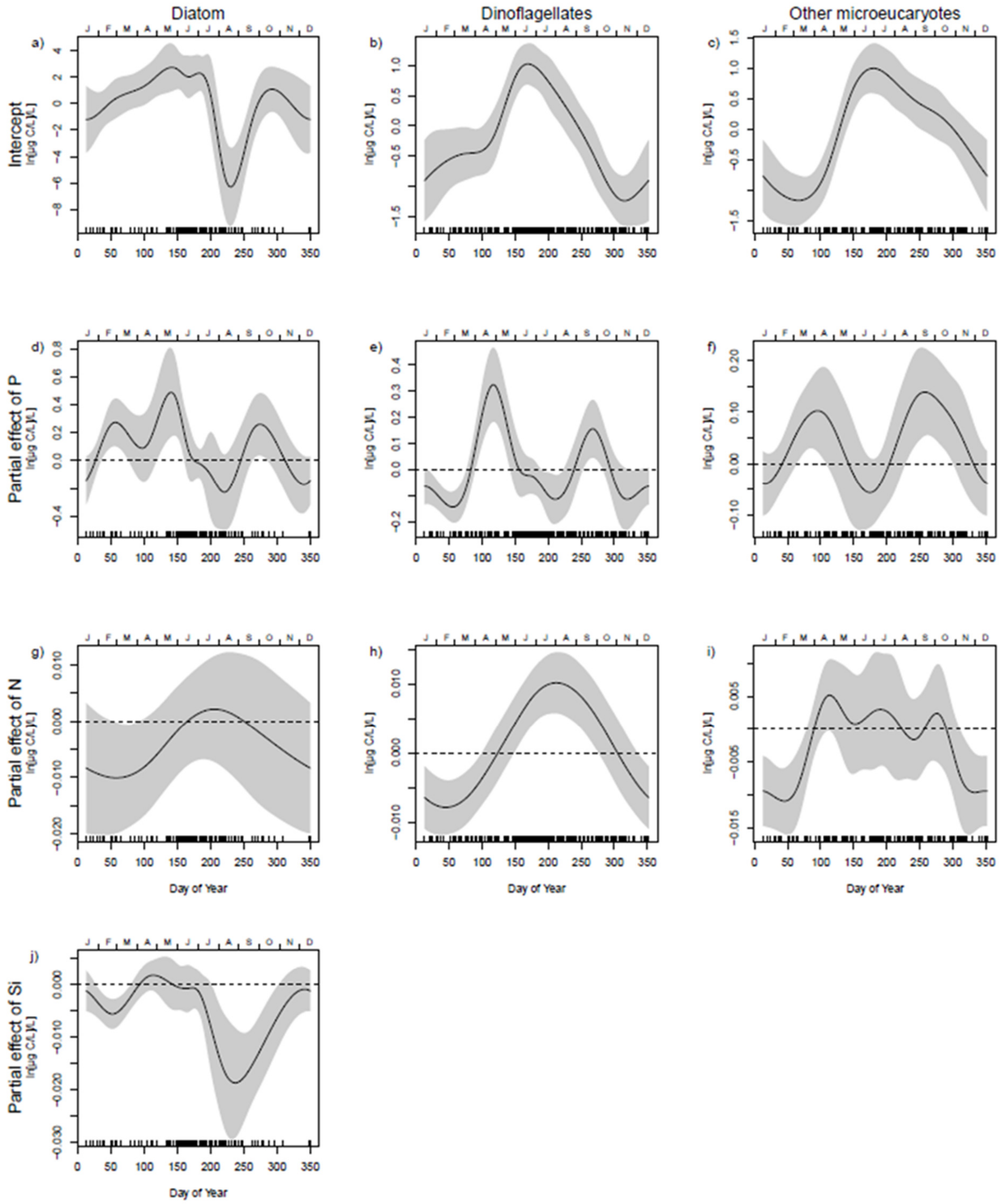


*Figure 8:Seasonally varying coefficient model showing the seasonal specific correlation between phytoplankton groups and nutrient estimated by model M4. a-c are the intercepts of each modelled group. d-j show the estimated ln-scale change in biomass for one-ln-unit increases in, respectively, phosphorus (P) (d-f), nitrogen (N) (g-i) and silicate (Si) (j) compared to the long-term averages of ln(P), ln(N) and ln(Si) or a given time of year. The stippled lines show the location of zero, corresponding to no correlation between biomass and P, N or Si.*

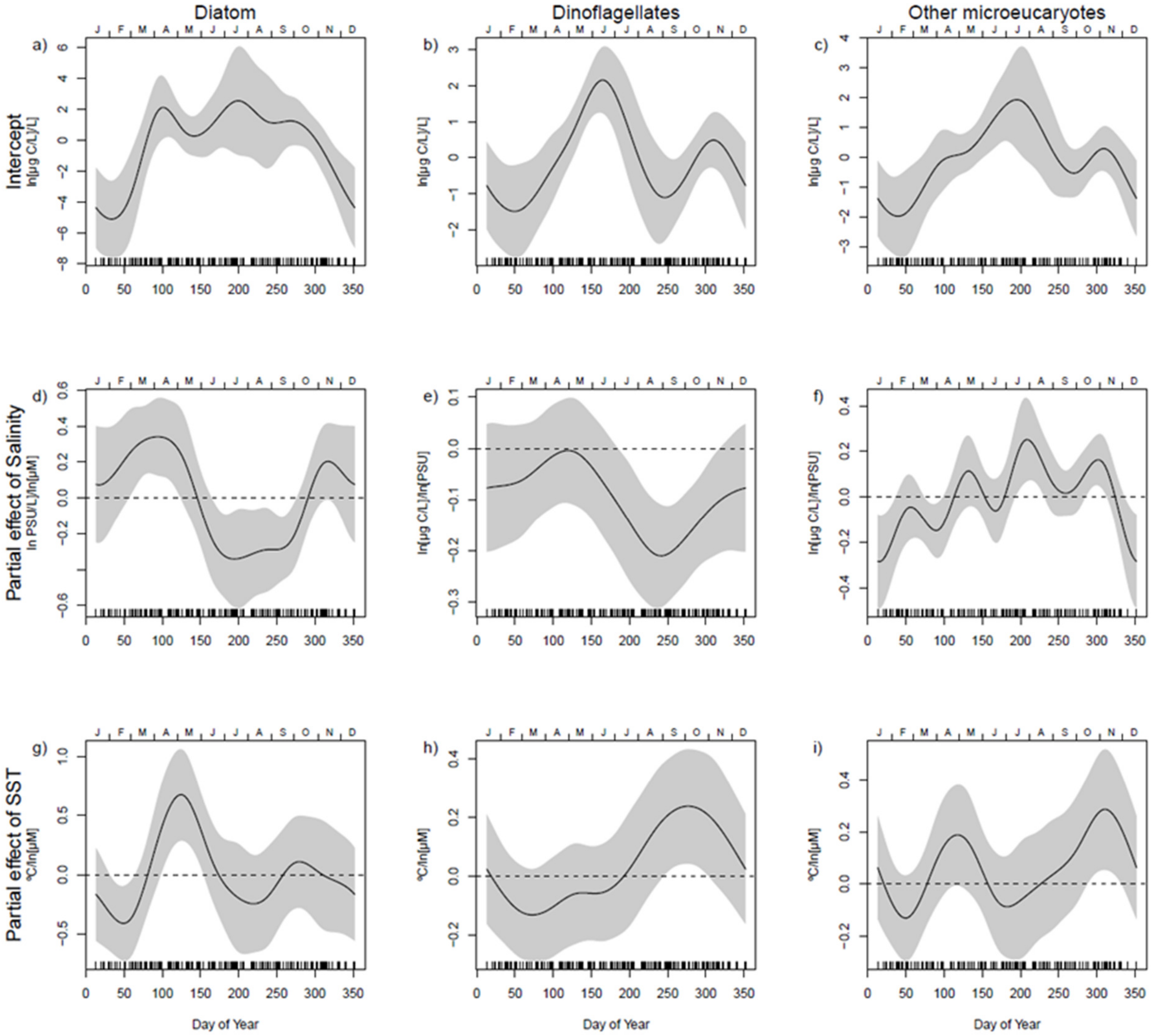


*Figure 9: Seasonally varying coefficient model showing the seasonal specific correlation between phytoplankton groups and salinity estimated by model M4. a-c) The intercepts of each modelled group. d-i) Estimated ln-scale change in biomass for one-ln-unit increases in, respectively, salinity (S) (d-f), and sea surface temperature (SST) (g-i) compared to the long-term averages of ln(S), and SST or a given time of year. The stippled lines show the location of zero, corresponding to no correlation between biomass and S and SST.*

In PAPER IV we analysed five stations in outer Oslofjorden to further investigate how potential climate-induced changes can impact the phytoplankton community. The five stations are situated from north to south along a salinity gradient, but an initial analysis showed that the phytoplankton phenology is comparable. The analysis showed that on average Secchi disc depth has increased, but the chlorophyll *a* levels have remained stable throughout the last 20 years.

When analysing the changes in seasonality over the years it was clear that the spring bloom had decreased, and the autumn bloom increased. The decrease in chlorophyll is followed by a decline in diatom abundance and is evident for most dominating diatom taxa apart from *Pseudo-nitzshia*. During the same period, there has been an increase in the abundance of dinoflagellates.

We found indications of decreased salinity and significant increased SST in the surface waters for the period 2000-2020.

We found a significant negative correlation between winter temperatures and diatom abundance when investigating the correlation between nutrients, temperature, salinity, and the different phytoplankton groups. This result indicates that high winter/spring temp gives lower diatom abundance and low winter, and spring temperatures gives higher abundances.

There is also a clear positive correlation between high salinity and high abundances of diatoms, indicating that low salinity and increased stratification leads to lower diatom abundances.

At one station, OF2, we also have records of zooplankton from the period 2007-2020. The seasonal and yearly patterns of zooplankton show that there has been a decrease in the zooplankton fraction larger than 1000 µm but an increase in the smaller zooplankton (180-1000 µm) (Figure 10). The smaller size groups are more abundant during spring, while in the summer and autumn, the larger ones have higher total biomass (Figure 10). The increase in smaller zooplankton occurs during summer, while there are indications of higher winter biomass since 2013 for the total biomass of zooplankton (Figure 11).

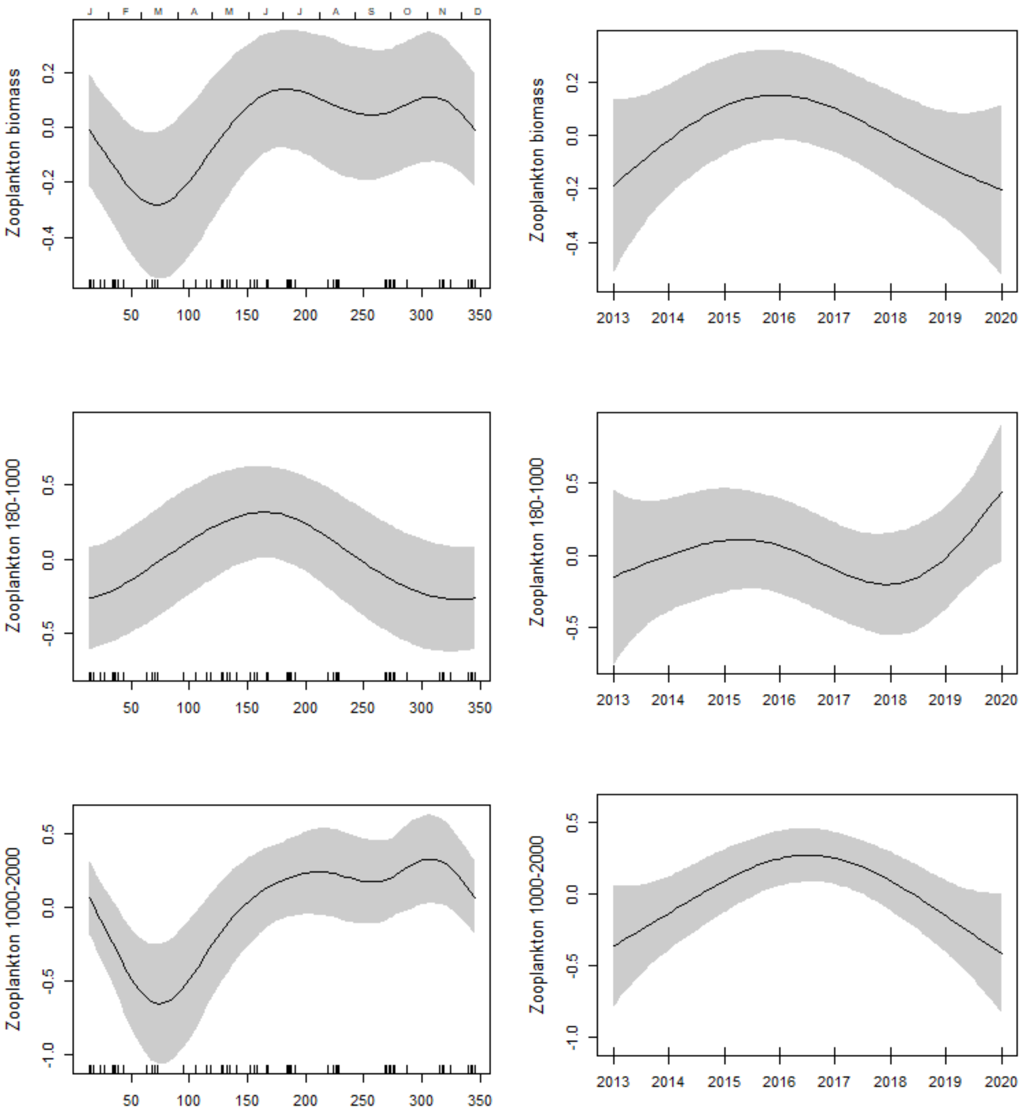


*Figure 10: Seasonal and yearly biomass of zooplankton from 2013 to 2020 estimated by model M2 in the outer Oslofjorden. Trend pattern is shown with 95 % confidence bands in grey.*

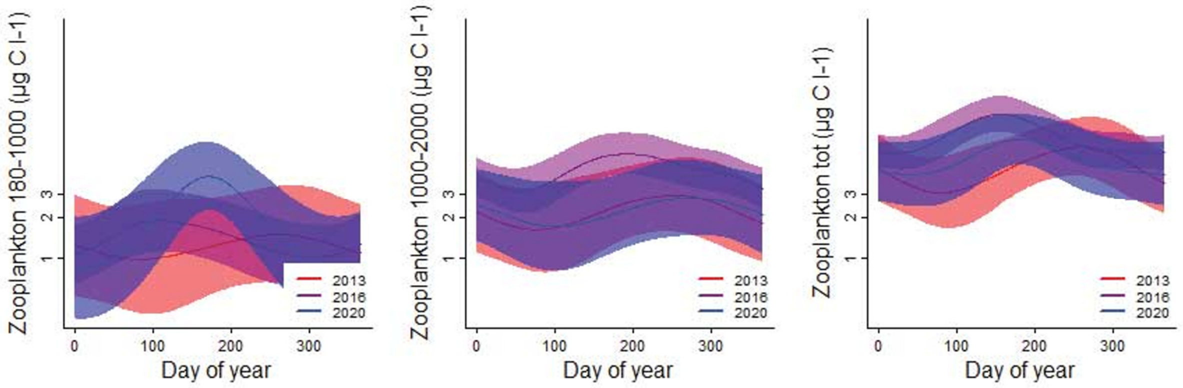


*Figure 11: Seasonal and yearly changes in abundance of calanoides, for the period 2013-2020, estimated by model M3 in the outer Oslofjorden. The solid line is the smoothed curve fitted by the GAM-model, and the light-coloured areas represent the 95% confidence bands.*

## DISCUSSION

The ecological situation in the Oslofjorden is under severe threat. Kelp forests and seagrass meadows are declining, and fish and seabird populations are critically low (Anon, 2021b). Phytoplankton has an essential function in the marine ecosystem, and changes in phytoplankton abundance, distribution, and biodiversity impact the whole ecosystem. With gathering this long-term dataset from the Oslofjorden, we have developed a database that makes it possible to explore time changes in a eutrophic coastal area. The extent of the dataset also made it possible to study some of the main drivers of these changes.

### Seasonal distribution of phytoplankton in Oslofjorden

There is a strong seasonal pattern in the phytoplankton blooms in the Oslofjorden, typical for high latitudes (Cloern and Jassby, 2010; Longhurst, 1995). During winter, the cooling of surface waters cause unstable water masses, and northern winds mix-up nutrient-rich deep waters. Then, in early spring, the water column stratifies due to solar heating and freshwater inputs. The first annual bloom is set off when light availability becomes sufficient for photosynthesis. The stratification keeps phytoplankton in the well-lit upper water masses and enhances phytoplankton growth rate (Moschonas et al., 2017). In Oslofjorden, the first spring bloom typically starts in March/April. Then there is often an early summer bloom in June, and an autumn bloom in September (PAPER II). This pattern is similar in both the inner and outer Oslofjorden (PAPER IV) and on the Swedish west coast (Skjevik et al., 2011). The timing of phytoplankton blooms has been relatively constant throughout the century (Braarud and Nygaard 1967).

The spring bloom typically starts with diatoms, followed by dinoflagellates and other micro-eukaryotes. All available registrations from 1897 to 2020 show a similar distribution of blooming groups throughout the year. However, both overall abundance and biomass and the phytoplankton phenology have changed over the study period (1933-2020) (PAPER III).

### Impact of changes in eutrophication

Oslofjorden can be sectioned into two parts: the inner more semi-enclosed area and the outer more open sea. However, they are connected through the Drøbak strait and under the same pressure from utilisation and urbanisation (Moland et al., 2021). There are historical differences both in the nutrient loads and in management practices. Nitrogen removal was implemented in sewage plants the inner Oslofjorden from 1997 and 2000, but not in the outer parts. Today, there is a net influx of nitrogen rich water from the outer fjord to the inner parts during summer (Staalstrøm et al., 2021). We have found that nitrogen is limiting growth of phytoplankton to a greater degree in the inner (PAPER II and PAPER III) compared to the outer Oslofjorden (PAPER IV). This implies that the nitrogen reducing measures implemented in the inner Oslofjorden have limited phytoplankton production (PAPER III).

The inner part of Oslofjorden has undergone extreme changes in nutrient supplies during the last century: from the beginning of sewage release in the surface layers to modern and extensive sewage cleaning. For a semi-enclosed fjord, like the inner Oslofjorden, eutrophication effects on the phytoplankton community were evident as early as the beginning of 1900s (Braarud and Bursa, 1939; Hjort and Gran, 1900). Already in the 1930s, a very high abundance of phytoplankton was found, especially during summer. The coccolithophore *Emiliania huxleyi* often dominated summer plankton (Braarud, 1969). Extensive *E. huxleyi* blooms were common in inner Oslofjorden with numbers as high as 12 million cells $L^{-1}$ (Birkenes and Braarud, 1952). As a result of the decrease in nutrient supply, the abundance of *E. huxleyi* has continuously declined in the last 30 years. Since 2007, there have not been any records of *E. huxleyi* blooms above 5 million cells $L^{-1}$ in the inner Oslofjorden (PAPER III).

The chlorophyll levels, phytoplankton biomass, and abundance in inner Oslofjorden decreased tenfold in the period 1973-1990 (PAPER II, PAPER III). Concurrently, the amount of nutrients in surface water has also declined. Phosphorus levels decreased rapidly from 1980 until around 1998 but have since increased again. Even if the amount of nutrients cannot be linearly correlated to a reduction in primary production (Lenhart et al., 1997), the reduced nutrient loads are likely to impact the significant chlorophyll *a* decrease. Our results indicate that phosphorus controls the spring bloom amplitude and the reduced phosphorus concentration contributed to the decline in chlorophyll from the 1980s to the 1990s. However, the increase in phosphorus since the 2000s seems not to have led to increased chlorophyll levels, possibly because of limitation from the low nitrogen (PAPER II).

Further we analysed how these changes have impacted the phytoplankton community. The analysis reveals that diatoms are a key group in driving this change and shows how the reduction in diatoms corresponds to decreasing levels of nutrients. However, dinoflagellates do not have the same reduction as diatoms in the Oslofjorden (PAPER III). Dinoflagellates have advantageous strategies over diatoms to utilise phosphorus in phosphorus limited environments (Martínez-Soto et al., 2015). They also have the ability of mixotrophy and have low requirements of silicate. Due to their capability of vertical migration, they may also exploit nutrients from deeper water. These strategies may be why dinoflagellates do not have the same reduction in biomass as diatoms during spring, but a rather small decrease during summer and early autumn. In PAPER I we found clear indications that phytoplankton biomass was nitrogen-limited during summer and autumn. We suggested that the continuous reduction in nitrogen was the main controlling factor of the decreasing chlorophyll trend. Further analysis indicates that dinoflagellates are most affected by nitrogen limitation during summer and autumn (PAPER III). Due to the implementation of nitrogen cleaning measures, there has been a continuous decrease in the supply of nitrogen in inner Oslofjorden, which is often found to control coastal eutrophication (Howarth and Marino, 2010). Interestingly, in the outer Oslofjorden where nitrogen removal is not implemented in the sewage treatment, the dinoflagellate abundance has increased since 1990, while the diatoms have decreased, similar to inner Oslofjorden (PAPER IV).

### Impact of a warmer climate

Changes in nutrient loads can explain the overall changes in phytoplankton biomass and abundance found in Oslofjorden. However, there are also indications of changes that cannot be fully explained by eutrophication.

Our analysis shows that the onset of the first spring bloom started progressively later during the last 15 years. From 2006 to 2020 the analysis has shown that a delayed start to the spring bloom co-occurred with increasing SST in winter and spring. The study showed how the positive association between high SST and delayed spring bloom was linked to diatoms. Similar correlations between high SST and decreasing phytoplankton biomass have been found in experimental studies (Sommer and Lengfellner, 2008) and between high winter temperatures and delayed spring bloom (Borkman and Smayda, 2009). In addition, reduced phosphorus levels in winter and spring may have contributed to earlier termination of the spring bloom, as supported by the interannual correlation analysis that suggested that diatoms can be limited by phosphorus during the spring bloom. This correlation corresponds to the reduction in chlorophyll *a* levels in inner Oslofjorden proposed to be due to phosphate limitation (PAPER II). Therefore, the reduced diatom growth in early March may be caused by a combined effect of increased SST during winter and phosphate limited growth of diatoms during early spring. There is a rise in silicate levels, primarily during spring, probably caused by reduced utilisation from diatoms (PAPER III).

All available registrations from 1897 to 2020 show a spring bloom dominated by diatoms and dinoflagellates in March. The reduction in biomass for diatoms since 2006, corresponds to decreasing levels of nutrients. However, dinoflagellates do not have the same reduction as diatoms in the inner Oslofjorden. In the outer Oslofjorden, there is an increase in the abundance of dinoflagellates during spring (PAPER IV). We argue above how dinoflagellates have advantages above other microalgae due to different strategies to utilise nutrients. But a shift towards a more dinoflagellate dominated spring bloom can also be linked to warmer winters, especially in coastal areas (Klais et al., 2011).

An increase in Secchi-depth has followed the decrease in phytoplankton abundance and biomass. As the high biomass of phytoplankton is a major cause of reduced water clarity, this relationship is expected. However, the trends in Secchi-depth do not strictly follow the trends in chlorophyll (PAPER II). We have suggested that a possible explanation is increased outflow of dissolved organic matter run-off from rivers, which has increased, especially in the eastern part of Norway during the period from 1986 to 2013 (Finstad et al., 2016) and led to the darkening of coastal water (Aksnes et al., 2009). However, in the outer Oslofjorden, there is an apparent increase in Secchi-depth, which was not expected (PAPER IV).

*Skeletonema* is the major driver of the delay in spring bloom in our study. The first annual peak in *Skeletonema* has weakened and been moved towards the peak in *Chaetoceros*. The first seasonal peak in *Chaetoceros* has been at the same time through the 15 years of in-depth studies. All dominating diatom taxa have decreased in abundance since 1990, but only *Skeletonema* have had a significant decrease in biomass in the last 15 years.

A long-term declining trend in *Skeletonema* abundance is found in other areas where nutrient levels are decreasing, e.g. Narragansett Bay (Borkman and Smayda, 2009). The authors found the strongest correlation between this reduction and an increase in water temperature and grazers, with significant correlations with reductions in phosphorus and silicate. The short-term analysis of zooplankton biomass from one station in outer Oslofjorden show indications of higher abundances during winter and early spring, but the results are not conclusive (PAPER IV).

## FUTURE PERSPECTIVES

During this study, we have compiled an extensive dataset comprising phytoplankton counts, chlorophyll and environmental variables in the inner Oslofjorden. Many of these data have not previously been publicly available. We have shown that this dataset can be used to analyse and understand the changes in the pelagic environment in a eutrophic environment. This work has given us some answers, but also new questions. We hope the compilation will facilitate more research to be conducted. We have found a correlation between increased temperature and changes in blooming patterns but have not yet succeeded in fully understood the mechanisms that control these changes. Further, we want to study the implication of stratification and possibly changes in the composition of phytoplankton species during the spring bloom. We should also connect to more data and expertise in zooplankton and fish to understand these changes' implications for the food web.

We also wanted to use the results for management purposes, but this work is still in progress.

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Journal of Sea Research 164 (2020) 101925

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

# Long-term coastal monitoring data show nutrient-driven reduction in chlorophyll

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ARTICLE INFO

*Keywords:*
Time series analysis
Ecosystem management
Oslofjorden
Eutrophication
GAM
Anthropogenic pressure

ABSTRACT

In this study we have compiled a long-term monitoring dataset from the inner Oslofjorden and supplemented it with short-term research data from the same station. Using generalized additive models analysing the data from this time series, we have examined how chlorophyll-*a*, hydrography, and various nutrient concentrations have changed during 1973–2017 and how they correlate. We describe the seasonality in chlorophyll-*a*, nitrogen, phosphorus, Secchi-depth, temperature and salinity and how the levels of each variable have changed the last forty years. The results show specifically how levels of chlorophyll-*a* have decreased significantly and how this correlates with decrease in nitrogen and phosphorus levels. Our results show a significantly positive correlation between chlorophyll-*a* and phosphorus during spring bloom and between chlorophyll-*a* and nitrogen during autumn bloom. However, phosphorus levels have increased again during the last 20 years, but chlorophyll-*a* levels are still low, indicating that the chlorophyll-*a* level currently may be controlled by the continuous decreasing trend in nitrogen. If nitrogen increase again, the chlorophyll-*a* level may also begin to increase. The impact of increasing temperature and possible change in starting point for the growing season should be studied further.

## 1. Introduction

Eutrophication is a major threat to coastal marine ecosystems worldwide, and has been known as such for more than 50 years (Ryther and Dunstan, 1971). Increased supply of nutrients to the ecosystem causes increased phytoplankton production and can lead to reduced surface water quality (Nixon, 1995; Paasche and Erga, 1987). Sinking plankton biomass can further contribute to oxygen consumption and thereby lower oxygen levels in the deeper basins (Cloern, 2001; Staalstrøm, 2015). Eutrophication may also lead to an increased occurrence of toxic algal blooms (Heisler et al., 2008).

Phytoplankton seasonality is primarily controlled by light, nutrient availability, and stratification. In temperate marine environments, phytoplankton phenology is dominated by two bloom events (Longhurst, 1995). During winter, when growth is limited by light and water masses are unstable, the density of phytoplankton is low. Spring bloom starts when increased daily irradiance and increased stratification cause phytoplankton to grow rapidly in the upper mixed layer on nutrients supplied by prior turbulence and convective mixing of the upper water column (Erga and Heimdal, 1984; Kristiansen et al., 2001; Sverdrup, 1953). The spring bloom ends by combined effects of nutrient depletion, grazing, and sometimes viral control (Erga, 1989; Kristiansen et al., 2001; Larsen et al., 2004). In the inner Oslofjorden, as in other Norwegian fjords, it is also common to have a second bloom in May or June when snow is melting in the highlands and nutrient-rich melting water is reaching the coast (Paasche and Erga, 1988). The autumn bloom occurs when and if seasonally increasing vertical mixing (convective cooling and winds) renews the nutrient supply in the euphotic zone before light availability becomes limiting (Findlay et al., 2006; Paasche and Ostergren, 1980).

The water quality of the inner Oslofjorden is believed to have improved significantly from the 1960s until today and the fjord, which was found polluted and unattractive by the general public until the 1990s can be considered a summer paradise today with appealing beaches and swimming facilities close to the city centre (Baalsrud and Magnusson, 2002). The fjord is used both for transportation and recreation for a growing population, and it is the main recipient of wastewater for the city of Oslo, the capital of Norway. Records from as

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https://doi.org/10.1016/j.seares.2020.101925
Received 5 December 2019; Received in revised form 19 June 2020; Accepted 2 July 2020

early as the 1900s describe increased phytoplankton abundance attributed to the supply of nutrients in the near city and the harbour areas (Braarud, 1969). The release of wastewater sewage into the fjord increased dramatically after the introduction of water closets around 1900, and the first sewage plant (Skarpsno) was built in 1911. This sewage plant provided only physical cleaning, but later Skarpsno was the first sewage treatment plant with chemical removal of nutrients (phosphorus), which was introduced in 1975 (Baalsrud and Magnusson, 2002). From this time and onwards, more sewage plants were built, and gradually more of the wastewater was collected and treated. Nitrogen removal by biological treatment was established in the first plant (VEAS) in 1997, and the last one (Bekkelaget) in 2000 (Baalsrud and Magnusson, 2002).

Eutrophication impact on the phytoplankton community in the Oslofjorden has been documented through surveys from the early 1900s (see Braarud, 1969). An extensive survey was carried out by the University of Oslo in 1933–34, which showed that the seasonal patterns of phytoplankton were very different in the inner and outer parts of the fjord and that this was caused by the nutrient loads (Braarud, 1945). An extensive study conducted in 1962–64 documented that the upper water column was heavily eutrofied, and nutrient supply from land-based activities was one of the main sources causing this problem (Munthe-Kaas, 1968). Therefore a monitoring program of the water quality in inner Oslofjorden started in 1973 and is still ongoing (Lundsør et al., 2018; Magnusson and Källkvist, 1974a).

Maintaining a good environmental status is one of the major prerequisites for the ecosystem to be able to provide the necessary habitat for marine organisms (Dickey-Collas et al., 2017). Knowledge about the dynamics of the phytoplankton community and phenology is a prerequisite for the understanding of processes and drivers of changes in the marine ecosystem (Johannessen, 2014). Chlorophyll-*a* is commonly used as a proxy for phytoplankton biomass and as an indicator of environmental status. Chlorophyll-*a* levels above a specified threshold (area-specific) are an indication of reduced water quality. The EU Water Framework Directive (WFD, 2000/60/EC) has set a requirement that water should be of “good” to “very good quality,” as measured by various ecological parameters (Borja et al., 2010). Norway adopted the WFD in 2000, and the Norwegian Environment Agency published the first national guidelines in 2013. The evaluation of the ecological status of pelagic waters of the inner Oslofjorden in 2018 (Lundsør et al., 2018) states that chlorophyll-*a* levels qualify for “good to moderate” ecological conditions by the WFD (Direktoratsgruppen vanndirektivet, 2018).

Increased knowledge about the causes of observed changes in chlorophyll-*a* is fundamental for the management of the Oslofjorden and other coastal waters under pressure. To determine if such changes are caused by anthropogenic pressures or by natural variability is, however, difficult in habitats with high variability in salinity, temperature, and light (Elliott and Quintino, 2007), and require long-term observations of chlorophyll-*a* as well as potential drivers of the changes. Therefore we have used data from the monitoring program and previous research projects where chlorophyll-*a*, nutrients and hydrography data have been collected for 45 years. This time series provides a unique opportunity for studying and better understanding the effects of climate and eutrophication on changes in chlorophyll-*a*.

This study aimed to understand how chlorophyll-*a* levels have changed over time and investigate the causes of these changes. In particular, we wanted to determine how nutrient levels, together with temperature and salinity, control chlorophyll levels through the year (seasonality) and over the years. To accomplish these goals, we used generalized additive models (GAM) and determined how the key environmental variables temperature, salinity, Secchi depth, and various nutrient concentrations have changed with the season and over the years. This knowledge is necessary to understand how anthropogenic impact contributes to eutrophication and changes in phytoplankton biomass, which is fundamental for knowledge-based long-term management of temperate fjord systems.

## 2. Material and methods

### 2.1. The study area

The inner Oslofjorden is a sill fjord of 190 km$^2$ size (Baalsrud and Magnusson, 2002). The connection to the more open outer Oslofjorden and Skagerrak is through the narrow sound of Drøbaksundet, where the sill is as shallow as 19.5 m. North of the Drøbak sill more sills divide the fjord into several basins, such as Vestfjorden, Bærumsbassenget, Bekkelagsbassenget, and Bunnefjorden. This bathymetry is a constraint to efficient deep-water renewal (Magnusson and Berge, 2015; Staalstrøm, 2015) that takes place in the inner Bunnefjorden basin only on average every 3–5 years (Baalsrud and Magnusson, 2002). In Vestfjorden, the deep-water exchange takes place every year.

Rivers and streams are the major sources of new bioavailable phosphate in the fjord, but the contribution from sewage treatment plants and overflow runoff is also significant (Vogelsang 2011). The limited deep-water exchange makes the fjord especially vulnerable to pollution, especially of nutrients and organic matter that may lead to high levels of oxygen consumption in the deep-water (Staalstrøm, 2015).

The Oslofjorden is a relatively sheltered area with calm weather. The prevailing winds are southerly or south-westerly in the summer and northerly during winter (Baalsrud and Magnusson, 2002). Long periods of northerly winds are favourable for water exchange since such winds pull the surface mixed layer southwards, thereby producing a water deficiency that facilitates the influx of oxygen-enriched, saline, and heavy Atlantic water northwards along the bottom and pass the sills. Climate changes seem to lead to weaker or shorter periods of these northerly winds that impact the frequency of deep-water exchange (Thaulow and Faafeng, 2014).

### 2.2. Compilation of historical water quality data from the inner Oslofjorden

The monitoring program of the inner Oslofjorden presently covers 22 stations. The sampling station Dk1 is one of the two major stations that are visited on all surveys and with the longest time series of data collected. It is situated in Vestfjorden at N 59.8149 E 10.5694 (west of the islands “Steilene”) and is 100 m deep (Fig. 1). The compilation of historical data was conducted in collaboration between Norconsult, University of Oslo and Norwegian Institute for Water Research (NIVA). The data used in this study are the variables temperature, salinity, nutrients, Secchi depth, and chlorophyll-*a* from monthly surveys. Water sampling methods have been either by a hand-held water sampler, Niskin water bottles attached to a CTD-rosette lowered to the sampling depths or a 2 m plastic Ramberg sampler for an integrated 0–2 m sample (Lundsør et al., 2018; Magnusson and Källkvist, 1974a).

Over time there have been different sampling regimes, and chlorophyll-*a* has been sampled at different standard depths, ranging from 0, 0–2, 4, and 5 m. We here used data from 0 m, which is the most common sampling depth in our material.

### 2.3. Hydrography, nutrients, and chlorophyll-*a*

Water samples have been collected from station Dk1 in the inner Oslofjorden by NIVA for “Fagrådet for vann- og avløpsteknisk samarbeid i Indre Oslofjorden” (Fagrådet) for most years since 1973 and by Norconsult for the years 2015–2018 (see Fig. 2 for data overview). Most data used were already digitalized, but the remaining were compiled from written reports in this study. For the years 1980–1981, Svein Kristiansen provided data from a study by Paasche and Kristiansen (1982).

Chlorophyll-*a* samples were analysed by a standard spectrophotometric method (Dahl and Sørensen, 1981) from early 1980s using

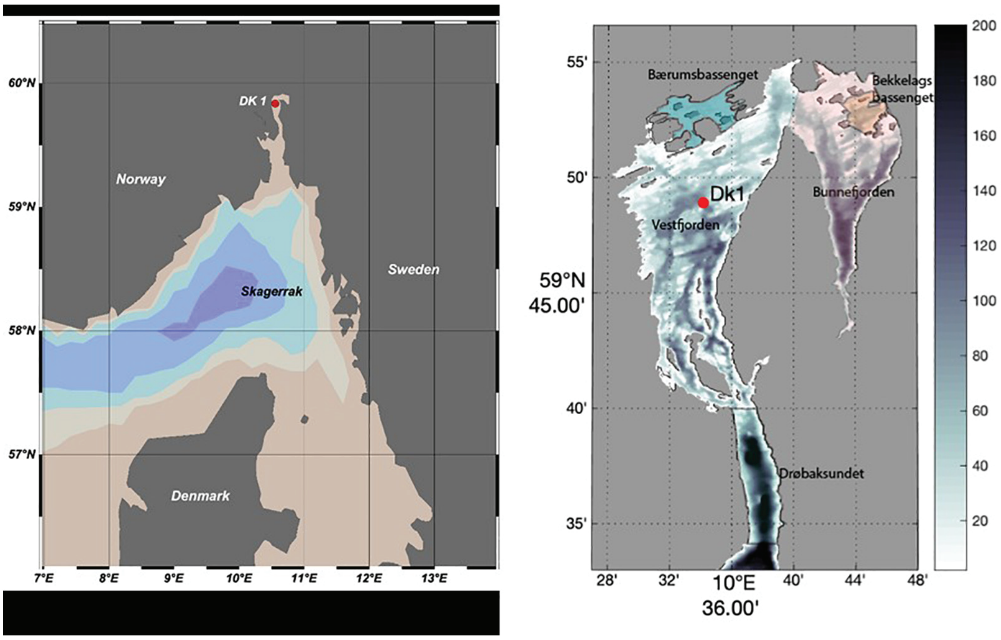

**Fig. 1.** Sampling station Dk1 (Steilene) in the inner Oslofjorden, Norway, a fjord of the Skagerrak.

a 90%-acetone extraction with homogenisation of the extract. This became later the Norwegian Standard NS 4766 (NS4766, 1983). Before 1980s NIVA used mainly in vitro fluorometric methods, either a FM3 or a Turner filterfluorometer, which were calibrated with the 90%-acetone spectrophotometric method using algal cultures. From 1989 the NS4766 method was replaced with the spectrophotometric 100% methanol extraction method following the Norwegian Standard NS4767 (NS4767, 1983) (Kai Sørensen, pers.com.). We here analysed the data on ln-scale (*logChl* = ln[µg/L chlorophyll-*a*]) to homogenize the variance.

Water for analyses of nutrient and chlorophyll-*a* concentrations was collected together and mostly from the same sampling bottles, which means that time and place are the same. The water samples were analysed in the laboratory by NIVA (1973–2014) and ALS Scandinavia in Oslo (2015–2018). The methodology for the analysis of dissolved, inorganic, and organic concentrations of total nitrogen (N) and total phosphorus (P) used from 1973 to 1984 (P) and to 1993 (N) was photo-oxidation with ultraviolet radiation (Henriksen, 1970). The Norwegian standard spectrophotometric methods for determination were implemented in 1984 for phosphorus and 1993 for nitrogen (NS 4725 and NS 4743). We here analysed data on ln-scale (*logN* = ln[µM total N], *logP* = ln[µM total P]), as we expected the response variable in the analysis, *logChl*, to be linearly related to *logN* and *logP*.

Sea surface temperature (SST, °C) was measured with a reversing thermometer until CTD measurements were used from 1985. Sea Surface Salinity (S, practical salinity units, PSU) was measured from water samples with a laboratory salinometer (Magnusson and Källkvist, 1974b) until 1985 when salinity was estimated from conductivity measured by CTD. We here analysed data on ln-scale (*logS* = ln[S]) to avoid undue large influence from a few low values. Secchi depth (*Secchi*, m) is measured by lowering a disk into the water and measuring what depth the plate becomes invisible, lowering further and hauling it up until it is visible again. The average depth of the two observations is measured by a standard white disk of approx. 30 cm in diameter. Measuring Secchi depth is a useful tool for checking vertical visibility in the water, and is used as a supplement to other variables in order to describe the water quality (Aas et al., 2014; Direktoratsgruppen vanndirektivet, 2018). We here analysed data on ln-scale (*logSecchi* = ln[m]) as we expected a linear relationship between *logSecchi* and *logChl*.

### 2.4. Statistical analyses

#### 2.4.1. Quantification of trends

To quantify and describe the seasonal and interannual trends in chlorophyll-*a*, nutrient levels and hydrographical factors, a non-parametric regression analysis was performed. Generalized additive models (GAMs) were used as implemented in the mgcv-package version 1.8–26 (Wood, 2017) in the statistical programming environment R version 3.5.1 (R Core Team, 2017).

Three models with different levels of complexity were considered for each response variable. The alternative response variables were $logChl_t$, $logSecchi_t$, $logN_t$, $logP_t$, $logS_t$, and $SST_t$ (in Eqs. (1)–(3) referred to by the generic notation $X_t$). The subscript *t* refers to time.

The predictor variables were day of the year ($D_t$) and year ($Y_t$). Model M1 (Eq. (1)) shows average seasonal patterns with the assumption of no trends between years:

$$X_t = a + f(D_t) + \varepsilon_t \tag{1}$$

Here, *a* is an intercept, *f* is a smooth function of *D* (a cyclic cubic spline, whose ends match to wrap the last day of the year to the first one in a seasonal cycle), and ε is an independent and normal distributed error term. Model M2 (Eq. (2)) includes trends between years but has the assumption of no changes in seasonal patterns over the years:

$$X_t = a + f(D_t) + g(Y_t) + \varepsilon_t \qquad 2$$

Here, *a*, *f* and ε have the same interpretation as in Eq. (1) but are estimated separately from that model, and *g* is a smooth function of *Y* (a thin plate regression spline, i.e., the default spline function in the mgcv package). Model M3 (Eq. (3)) includes seasonal and interannual trends and allows for possible changes in seasonal patterns over the years:

$$X_t = a + h(D_t, Y_t) + \varepsilon_t \tag{3}$$

Here, *h* is a two-dimensional tensor product smooth function of *D* and *Y* (a tensor product of two basis functions: a cyclic cubic spline function of *D* and a thin plate regression spline function of *Y*).

#### 2.4.2. The relationship between chlorophyll-a and environmental variables

In the second part of the analysis, we investigated how variation in nutrients and hydrographical variables could explain the variation in

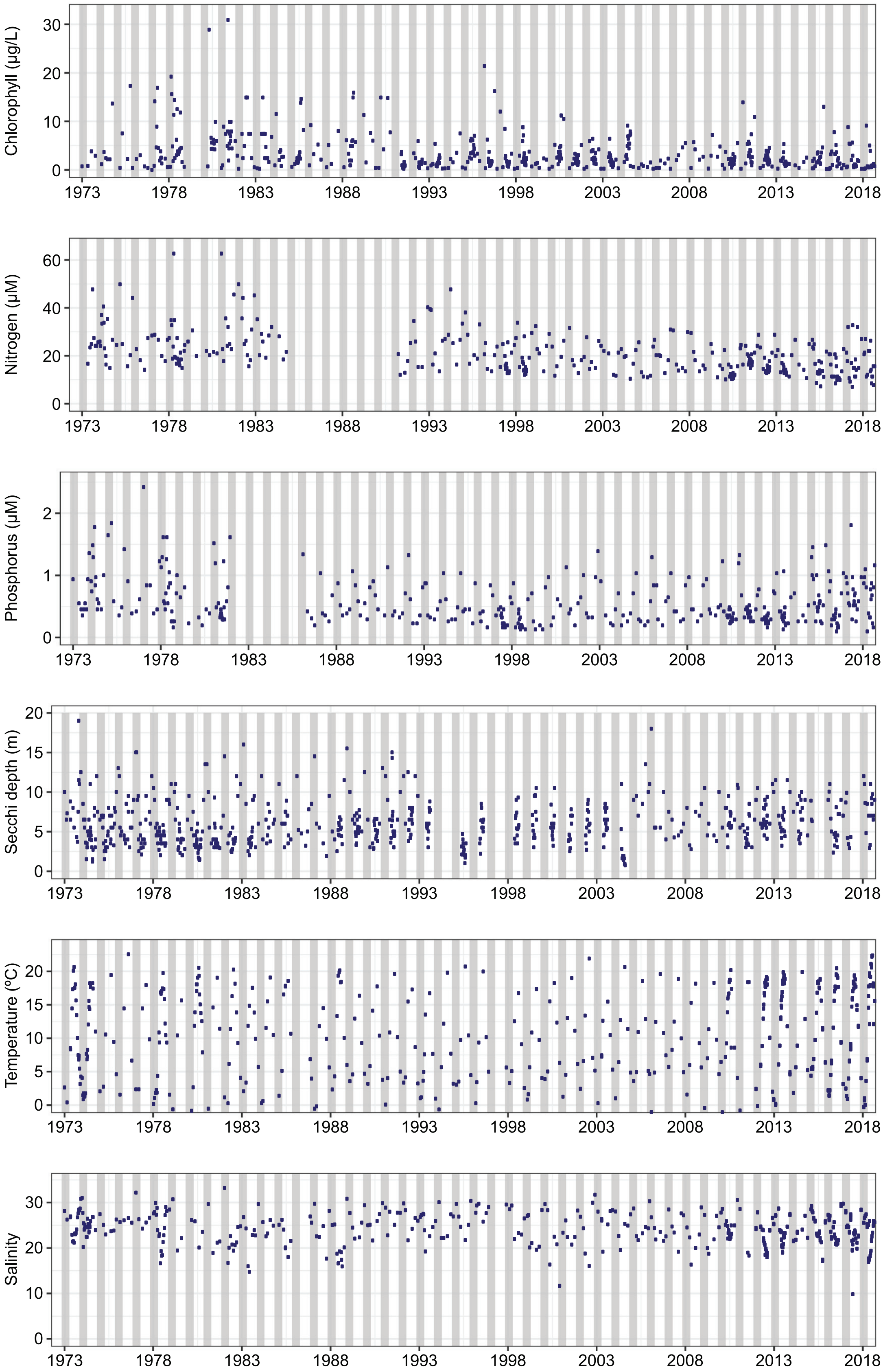

**Fig. 2.** Hydrographical surface data from station Dk1, inner Oslofjorden, Norway, used in this study. Dark areas indicate winter season from October to March.

chlorophyll-*a* levels. Model M4 (Eq. (4)) shows the seasonal correlation between levels of chlorophyll-*a* (*logChl*), phosphorous (*logP*) and nitrogen (*logN*):

$$logChl_t = b + k(D_t) + m(D_t)\cdot logPc_t + n(D_t)\cdot logNc_t + \varepsilon_t \tag{4}$$

Here, $b$ is the intercept, $k$, $m$ and $n$ are smooth (cyclic cubic spline) functions of *D*, *logPc* is *logP* centred by subtracting the mean, and *logNc* is *logN* centred by subtracting the mean. The function $k(D_t)$ gives the seasonal trend predicted for $logPc = 0$ and $logNc = 0$, that is, for mean values of *logP* and *logN*. The functions $m(D_t)$ and $n(D_t)$ give the season-dependent coefficients for, respectively, the effects of *logPc* and *logNc* on *logChl*. These two functions thereby show how the interannual correlations between *logChl* and *logP* and between *logChl* and *logN* change through the season.

Model M5 (Eq. (5)) shows associations between chlorophyll-*a* and nutrients as well as temperature and salinity:

$$logChl_t = c + o(logN_t, logP_t) + p(T_t, logS_t) + \varepsilon_t \tag{5}$$

Here, $c$ is the intercept, and $o$ and $p$ are two-dimensional smooth functions (tensor products of thin plate regression spline basis functions). This analysis was restricted to the part of the year when nutrients could be limiting the growth (day 100–300, April to October), as indicated by positive correlations between nutrient levels and *logChl* according to the results of model M4. In addition to the full model (Eq. (5)), we considered reduced models with either of the two-dimensional smooth functions omitted or replaced by one-dimensional thin plate regression spline smooth functions, $r(logN_t)$, $s(logP_t)$, $u(T_t)$ or $v(logS_t)$.

### 2.4.3. Model comparison and diagnostics

Alternative model formulations were compared based on the Akaike's Information Criterion (AIC) (Akaike, 1974), the generalized cross-validation score (GCV, Wood 2006), and the percentage of deviance explained ($R^2$). The AIC measures the trade-off between goodness-of-fit and model parsimony and the GCV is a measure of leave-one-sample-out prediction error. Models with low AIC and low GCV were preferred over models with higher AIC and GCV. Only differences in AIC of more than 2 were considered statistically significant. To assess if residuals were approximately normally distributed and homoscedastic, we inspected quantile-quantile normal plots of the residuals and plots of residuals versus each covariate; to assess for temporal dependency, we plotted the autocorrelation function of the residuals. To assess if multicollinearity among predictor variables led to serious variance inflation in models M4 and M5, we calculated the variance inflation factor (VIF). The VIF estimates how much higher the uncertainty of the parameter estimates is because of collinearity; high VIF (e.g., VIF > 5) indicates that predictor effects cannot be separated based on the data used (Sheather, 2009). For M4, we calculated the VIF for each month separately, based on month-specific linear models that jointly are equivalent to M4:

$$logChl_{t,i} = b0_i + b1_i\cdot logPc_{t,i} + b2_i\cdot logNc_{t,i} + \varepsilon_{t,i} \tag{6}$$

Here, $logChl_{t,i}$, $logPc_{t,i}$ and $logNc_{t,i}$ refer, respectively to mean values of *logChl*, *logPc* and *logNc* in year $t$ and month $i$, $b0_i$, $b1_i$ and $b2_i$ are regression coefficients (corresponding to the smooth functions $k$, $i$ and $n$ in Eq. (4)), and $\varepsilon_{t,i}$ is an error term. For M5 we calculated the VIF for a simplified model compared to Eq. (5) with linear and additive effects of *logN*, *logP*, *T* and *logS*.

## 3. Results

### 3.1. Overview of time series data

The sampling frequency and number of variables studied have varied slightly over time, depending on the aim of the surveys. Type of variables and sampling frequency at DK1, inner Oslofjorden are given in Fig. 2. The number of sampling events has varied from 5 to 22 per year.

### 3.2. Seasonality and long-term trends

To determine seasonal and yearly changes in chlorophyll-*a* levels and the environmental variables, i.e., temperature, salinity, Secchi disk depth, and nutrient concentrations, we first analysed the data with day of year (D) and year as explanatory variables.

Three alternative models were tested and compared (Table 1). The comparison shows that season alone (model M1) explains 16.5% of the variation in chlorophyll-*a*, 94% in SST (sea surface temperature), and between 24 and 58% of the variation in the other variables. When also including changes over the years (model M2), $R^2$ increases for all variables and especially for chlorophyll-*a*, phosphorus, and nitrogen. At the same time, the GCV score is reduced, and AIC reduced with more than 2, which implies that there are significant changes between the years. However, for all variables except phosphorus, the model that also allows changes in seasonal patterns between years (model M3) is best fit to explain the variations. In comparison with the previous two, this model reduces GCV score and AIC with more than a factor 2. $R^2$ increases to between 33.5 and 95.4%. This shows that there are both changes between years and in seasonal patterns over the years.

### 3.3. Chlorophyll-*a* long-term trends

The seasonal and interannual trends in chlorophyll-*a* estimated from model M2 are shown on a logarithmic scale in Fig. 3a and b. The seasonal trends represent the average seasonality from all years monitored from 1973 to 2017. The model indicated a seasonal cycle with a spring bloom in March/April, an early summer bloom in June and autumn bloom in September (Fig. 3a). Fig. 3b shows that chlorophyll levels increased in the 1970s to a peak around 1980, decreased during the 1980s, and remained low from the 1990s to today. In the 1970s, the chlorophyll level was commonly around 20 μg/L during the spring bloom and often above 10 μg/L during summer months. Blooming levels in the last years were mostly below 6 μg/L (Fig. 2a). The change over time was statistically significant, as evidenced by a reduction in AIC of more than 2 when comparing model M2 to model M1 (Table 1), as well as by the confidence bands of the year trend (Fig. 3b).

The best model in terms of AIC and GCV was the one assuming that not only has the overall chlorophyll-*a* level varied over the years but also that the seasonal pattern varied (i.e., M3, Table 1). This model shows that the relative magnitudes of the spring bloom, summer low and autumn bloom have varied over time, and also suggests a tendency of later spring blooms in later years (Fig. 3c, with estimated seasonal patterns in selected years shown in the supplementary Fig. S1).

### 3.4. Nutrients

The nitrogen model indicated a seasonal cycle with a constant decrease in the amount of total nitrogen from January until the last days of August (Fig. 4a), which coincided with the autumn bloom (Fig. 3). Fig. 4b shows that there has been a declining trend in the nitrogen level since 1982, and that the levels have continued to decrease throughout the investigated period. The change over time was statistically significant (Table 1, Fig. 4).

Similar to chlorophyll-*a* and Secchi depth, the best model in terms of AIC and GCV was the one considering that not only has the overall amount of total nitrogen varied over the years but also that the seasonal patterns have varied (i.e., M3, Table 1). Specifically, it appeared that summer levels of total nitrogen started to decrease already in the 1970s while the winter levels first started to decrease in the 1990s (Fig. 4c, Fig. S2).

The seasonal model for phosphorus (M1) indicated a seasonal cycle similar to nitrogen, with decreasing concentrations from the beginning of the year until September (Fig. 5a). However, for phosphorus, we see

**Table 1**

*Generalized Additive Model (GAM) results* of the three different seasonal models tested for each response variable (Eqs. (1)–(3)). Model M1 (Eq. (1)) shows average seasonal patterns with the assumption of no changes between years. Model M2 (Eq. (2)) includes changes through years but has the assumption of no changes in seasonal patterns over the years (i.e., effects of season and year are additive at the scale of the predictor-variable). Model M3 (Eq. (3)) shows both seasonal and yearly variations, allowing for changes in seasonal patterns over the years. Model performance was measured by the Generalized cross-validation (GCV) score, Akaike's Information Criterion (AIC), and percentage of deviance explained ($R^2$). All models are significant, with $p < .01$. The model with the lowest AIC and GCV is marked bold.

| Response | Model M1 | | | Model M2 | | | Model M3 | | |
|---|---|---|---|---|---|---|---|---|---|
| | AIC | GCV | $R^2$ | AIC | GCV | $R^2$ | AIC | GCV | $R^2$ |
| Chlorophyll-*a* | 1310 | 0.827 | 16.5% | 1251.8 | 0.735 | 27.7% | **1227.8** | **0.706** | 36.5% |
| Secchi depth | 802.1 | 0.168 | 24.2% | 748.5 | 0.154 | 30.8% | **740.1** | **0.152** | 33.5% |
| Phosphorus | 496.5 | 0.212 | 43.1% | **412.8** | **0.170** | 55.8% | 422.9 | 0.176 | 58.0% |
| Nitrogen | 190.8 | 0.099 | 32.1% | 65.5 | 0.070 | 53.6% | **61.5** | **0.069** | 55.7% |
| Salinity | −514.0 | 0.015 | 37.8% | −533.0 | 0.014 | 43% | **−541** | **0.014** | 46.6% |
| SST | 2260.5 | 2.623 | 94.1% | 2230.4 | 2.494 | 94.5% | **2166.9** | **2.247** | 95.4% |

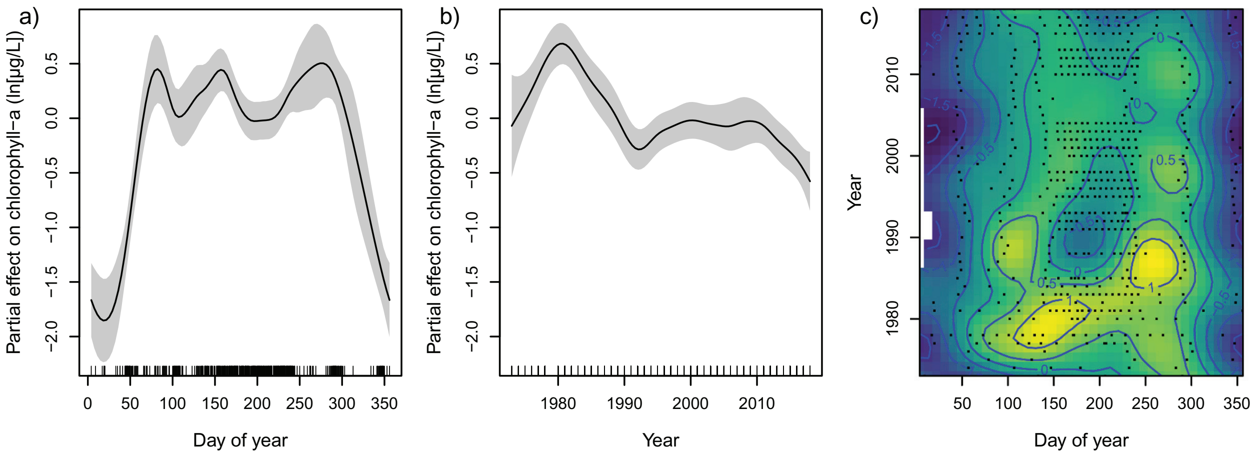

**Fig. 3.** Seasonal and yearly changes in chlorophyll-a level from 1973 to 2017 at station DK1 in the inner Oslofjorden estimated by model M2 (a and b) and M3 (c). Seasonal (a) and interannual (b) patterns are shown with 95% confidence intervals in grey. Combined seasonal and interannual patterns (c) are shown with lighter colours for higher levels of chlorophyll-a. The tick marks on the x-axes in panels a and b and the dots in panel c show the locations of the data. White areas in panel c are due to lack of data.

that the steepest decrease was from winter to April (Day 100), which coincided with the spring bloom (Fig. 3). Fig. 5b shows that there was a decline in the phosphorus level from 1973 to 1998 but that it has increased again after 2000. The change over time is statistically significant (Table 1, Fig. 5).

As model M2 was the best in terms of AIC and GCV (Table 1), the results indicated that the seasonality of phosphorus levels has not changed to the same degree as for other variables presented here.

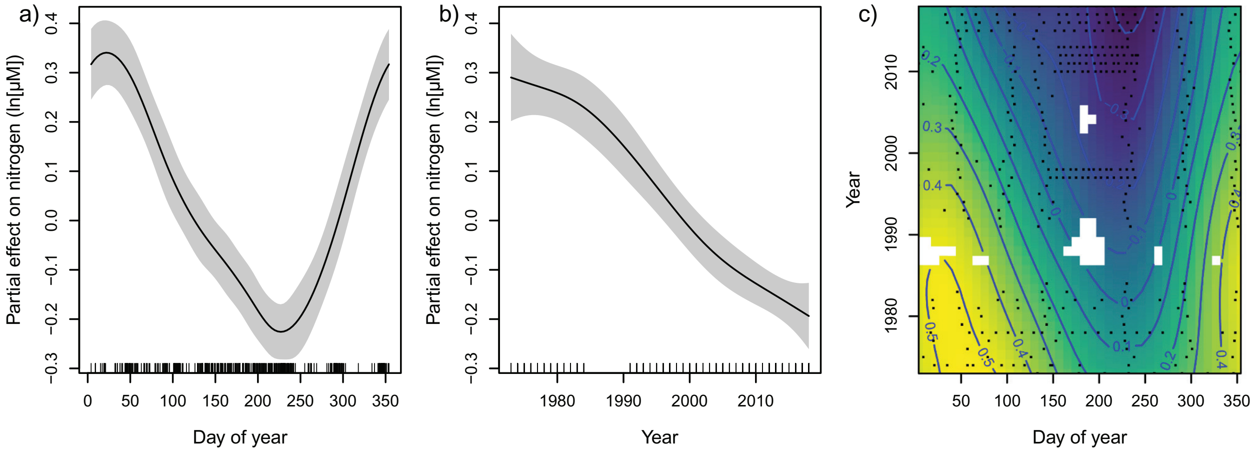

**Fig. 4.** Seasonal and yearly changes in nitrogen from 1973 to 2017 at DK1 (Steilene) in the inner Oslofjorden estimated by model M2 (a and b) and M3 (c). Seasonal (a) and interannual (b) patterns are shown with 95% confidence intervals in grey. Combined seasonal and interannual patterns (c) are shown with lighter colours for higher levels of total nitrogen. The tick marks on the x-axes in panels a and b and the dots in panel c show the locations of the data. White areas in panel c are due to a lack of data.

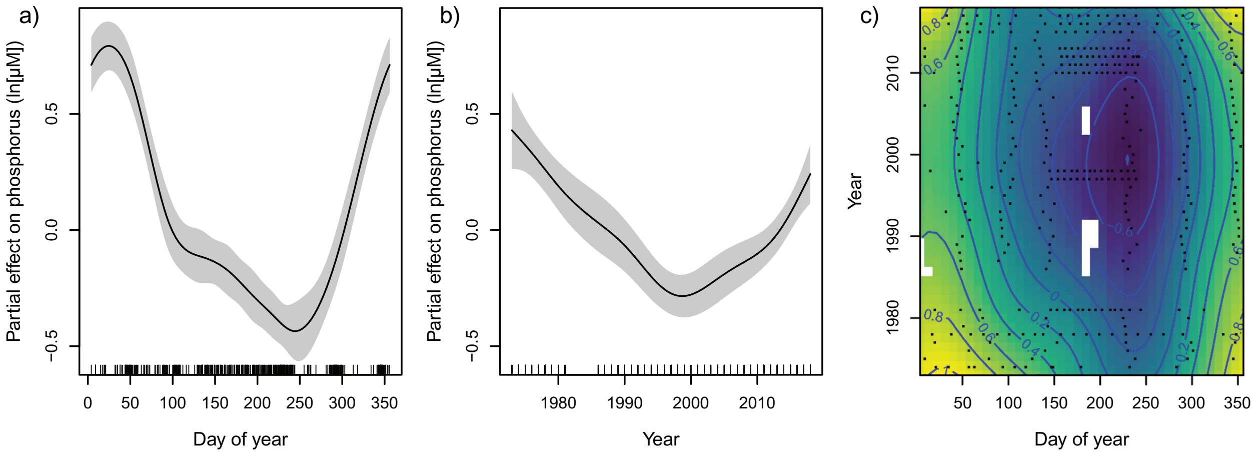

**Fig. 5.** Seasonal and yearly changes in phosphorus from 1973 to 2017 at DK1 (Steilene) in the inner Oslofjorden estimated by model M2 (a and b) and M3 (c). Seasonal (a) and interannual (b) patterns are shown with 95% confidence intervals in grey. Combined seasonal and interannual patterns (c) are shown with lighter colours for higher levels of total phosphorus. The tick marks on the x-axes in panels a and b and the dots in panel c show the locations of the data. White areas in panel c are due to a lack of data.

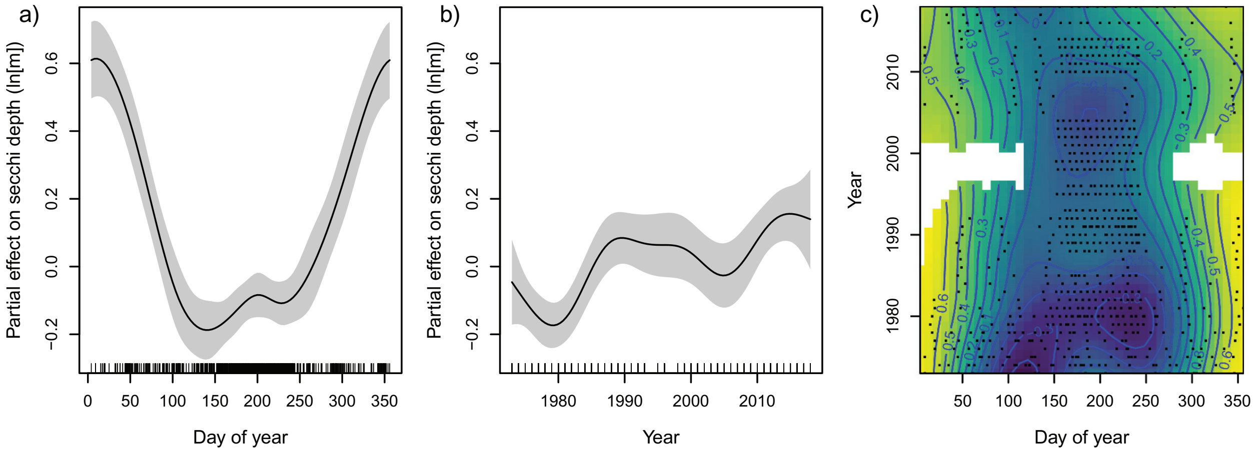

**Fig. 6.** Seasonal and yearly changes in Secchi depth from 1973 to 2017 at DK1 (Steilene) in the inner Oslofjorden estimated by model M2 (a and b) and M3 (c). Seasonal (a) and interannual (b) patterns are shown with 95% confidence intervals in grey. Combined seasonal and interannual patterns (c) are shown with lighter colours for higher levels of Secchi depth. The tick marks on the x-axes in panels a and b and the dots in panel c show the locations of the data. White areas in panel c are due to lack of data.

Consistent with this finding, we found that the phosphorus levels decreased in all seasons until 1998, when the levels started to increase again. Note that while the proportional changes were similar in all seasons, the changes in terms of µM phosphorus were largest in winter (Fig. 5c, Fig. S3).

### 3.5. Secchi depth

The analysis of Secchi depth data showed a seasonal cycle with decreasing Secchi depth from winter until the beginning of May, when the Secchi depth tended to be at the shallowest (Fig. 6a). The shallow Secchi depth was found to continue throughout the growing season with a slight increase during summer and a small decrease again during autumn bloom. Fig. 6b shows that there has been a trend towards deeper Secchi depth, starting in 1980. The best model in terms of AIC and GCV was the one considering that not only has the overall Secchi depth level varied over the years but also that the seasonal pattern varied (i.e., M3, Table 1). This model showed that the period with low Secchi depth in summer generally became shorter during the 1980s and 1990s, and also suggested a tendency of earlier increase in turbidity during the last ten years (Fig. 6c, Fig. S6. Comparison between yearly pattern of Secchi depth (Fig. 3b) and chlorophyll-*a* (Fig. 3b) showed that there was an inverse relationship between these two variables, with low values for Secchi depth and high chlorophyll-*a* levels during the 1970s and 1980s, but in later years, generally but not always, coinciding with high chlorophyll-*a* levels.

### 3.6. Temperature and salinity

Sea surface temperature and salinity showed opposite seasonality, with SST increasing and salinity decreasing from winter to summer (Figs. 7a and 8a). Fig. 7b shows that there has been an increase in SST from 1973 to 2017. This change over time was statistically significant (Table 1, Fig. 7b). For salinity, the change over the years was statistically significant (Table 1) but with no clear long-term trend (Fig. 8b).

As for most of the other variables, the best models for SST and salinity were the ones considering changes over the years in seasonal patterns (i.e., M3, Table 1). These models suggested a tendency of more pronounced increase in winter than summer sea surface temperatures (Fig. 7c, Fig. S5), and variability between years in the timing of spring reduction and autumn increase in sea surface salinity (Fig. 8, Fig. S6).

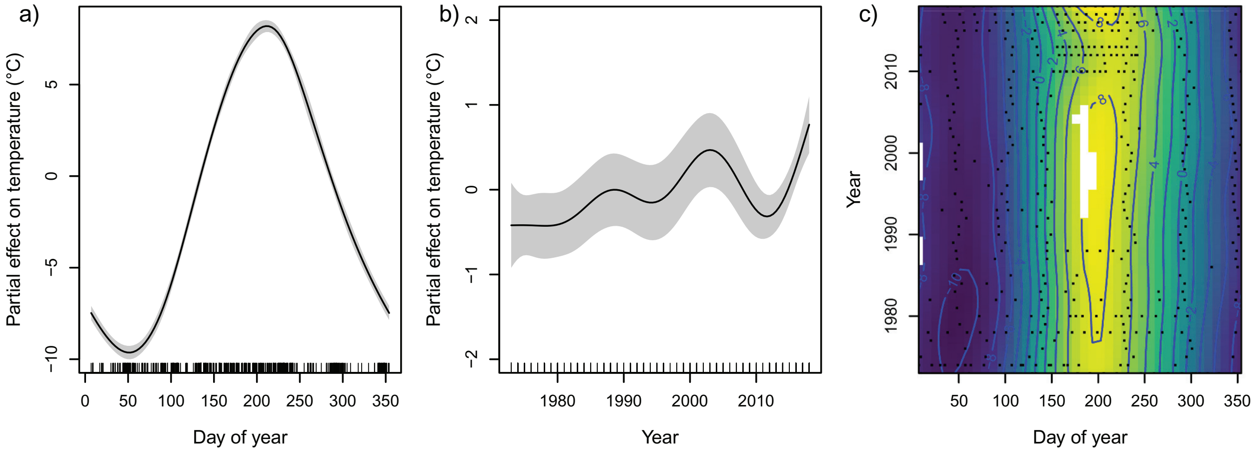

**Fig. 7.** Seasonal and yearly changes in sea surface temperature (SST) from 1973 to 2017 at DK1 (Steilene) in the inner Oslofjorden estimated by model M2 (a and b) and M3 (c). Seasonal (a) and interannual (b) patterns are shown with 95% confidence intervals in grey. Note the different y-axis scales. Combined seasonal and interannual patterns (c) are shown with lighter colours for higher temperature levels. The tick marks on the x-axes in panels a and b and the dots in panel c show the locations of the data. White areas in panel c are due to lack of data.

### 3.7. Correlation between chlorophyll-a and nutrient levels

The interannual correlation between the levels of chlorophyll-*a* and total phosphorus dependent on the day of year is shown in Fig. 9b. During the winter (October to February), there was a negative correlation that was changing to a strong positive correlation in April–May, which was the time just after the spring bloom. A significantly positive correlation in May was also shown by a linear model using only data from this month (Table S1). From June through November the correlation was close to zero. The total nitrogen levels showed a positive correlation with chlorophyll-*a* throughout the growth season (March–October) (Fig. 9c) and decreased slowly after that until the end of the growth period in October/November. The correlation between chlorophyll-*a* and total phosphorous was only significantly positive during the first blooming (spring bloom), while the positive correlation between chlorophyll-*a* and nitrogen was significantly different from zero from June to October. The magnitude of collinearity between the nutrient variables was checked by calculating the variance inflation factor (VIF). VIF was 2.15 for February and below 1.6 for all other months (Table S1), which is well below the cut-off value of 5 often used (Sheather, 2009).

### 3.8. Which environmental variables best explain the changes in chlorophyll-a?

The aim of the analysis using model M5 was to explore which environmental drivers were associated with the changes in chlorophyll-*a* over the years. The results showed that the full model, including total nitrogen, phosphorus, temperature as well as salinity as predictors of chlorophyll-*a*, was best in terms of GCV, AIC, and $R^2$ (Table 2). The interaction effect of total nitrogen and phosphorus showed that both these nutrients contributed to explain variations in chlorophyll-*a* and suggested that low levels of either nutrient could lead to reduced chlorophyll-*a* (Fig. 10a). The highest chlorophyll-*a* levels (bloom) were observed when both nutrients were at high levels. The interaction effect of SST and salinity showed that chlorophyll-*a* levels were low in typical winter situations when temperatures were low, and salinity was high. The highest chlorophyll-*a* levels were observed at temperatures around 10 °C and high salinities, which is typical for the spring situation when water is mixed and just starting to get stratified (Fig. 10b). The data available for this model are scarce, and it may be less robust than the previous models. VIF was below 2.6 for all variables (Table S2) which is below the cut-off of 5 and considered acceptable.

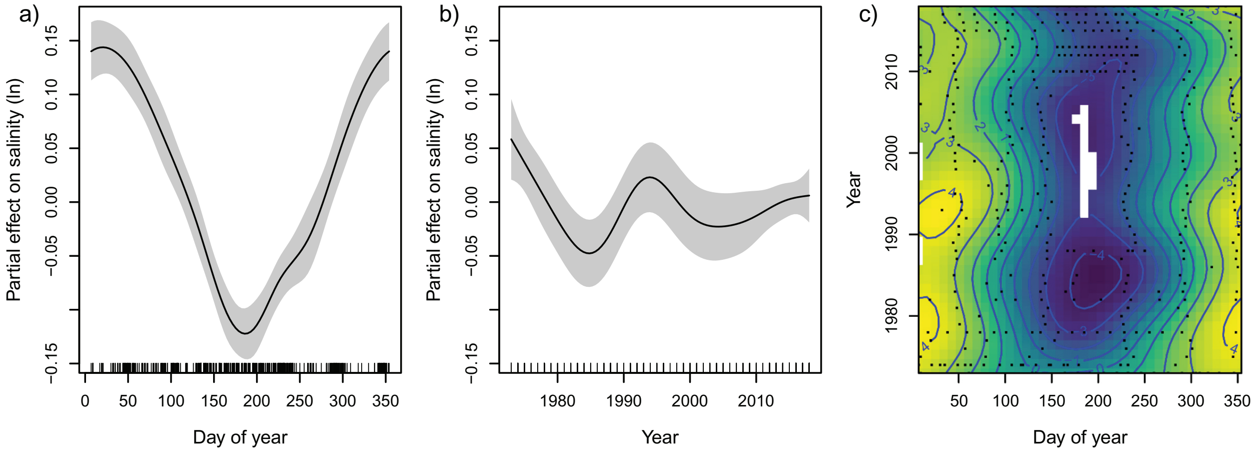

**Fig. 8.** Seasonal and yearly changes in sea surface salinity from 1973 to 2017 at DK1 (Steilene) in the inner Oslofjorden estimated by model M2 (a and b) and M3 (c). Seasonal (a) and interannual (b) patterns are shown with 95% confidence intervals in grey. Combined seasonal and interannual patterns (c) are shown with lighter colours for higher salinity levels. The tick marks on the x-axes in panels a and b and the dots in panel c show the locations of the data. White areas in panel c are due to lack of data.

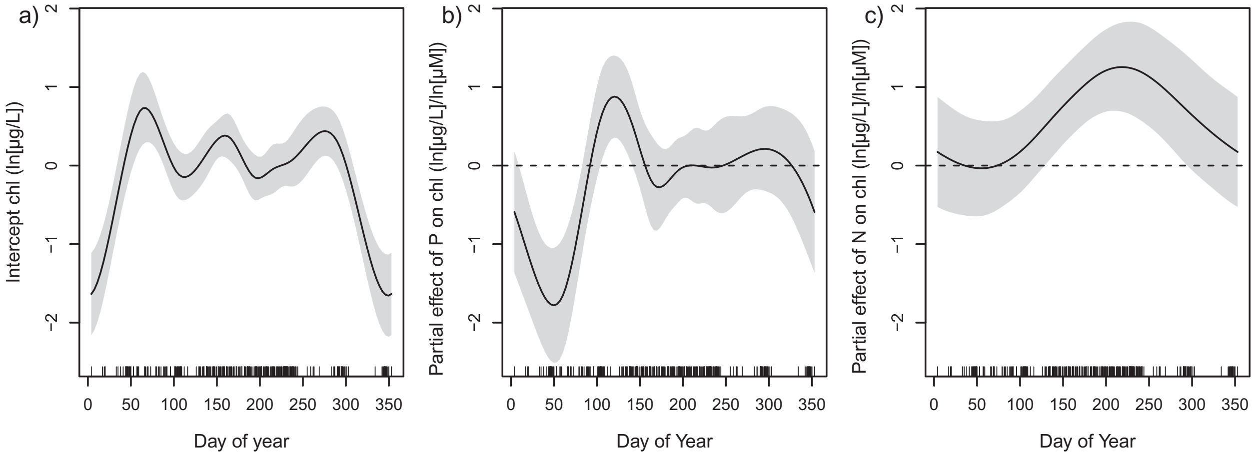

**Fig. 9.** Seasonally varying coefficient model showing the seasonal specific correlation between chlorophyll-a and total phosphorus (panel b) and nitrogen (panel c) estimated by model M4. Panel a) is the intercept. Panels b and c show the estimated ln-scale change in chlorophyll-a for one-ln-unit increases in, respectively, phosphorus (P) and nitrogen (N) compared to the long-term averages of ln(P) and ln(N) for a given time of year. The stippled lines show the location of zero, corresponding to no correlation between chlorophyll-a and P or N.

**Table 2**

Generalized Additive Model (GAM) results for effects of nitrogen (logN), phosphorus (logP), temperature (T) and salinity (S) on chlorophyll-a (logChl). The table shows Generalized cross-validation (GCV) score, percentage of variance explained ($R^2$, %), and Akaike's Information Criterion (AIC) for the full as well as for reduced models (Eq. (5)). Only models with all terms statistically significant ($p < .05$) are shown. The best model is marked bold.

| Predictor functions | GCV | $R^2$ | AIC |
|---|---|---|---|
| $o(logN_t, logP_t) + p(T_t, S_t)$ | **0.499** | **37.4%** | **300.9** |
| $o(logN_t, logP_t) + u(T_t)$ | 0.510 | 32.0% | 304.5 |
| $o(logN_t, logP_t)$ | 0.556 | 23.6% | 316.8 |
| $p(T_t, S_t)$ | 0.644 | 14.5% | 337.3 |
| $r(logN_t) + p(T_t, S_t)$ | 0.513 | 32.6% | 305.2 |
| $s(logP_t) + p(T_t, S_t)$ | 0.571 | 26.5% | 320.1 |

### 3.9. *Variability of predicted chlorophyll-a during five decades*

To further explore the relative roles of nutrients (N and P) and physical factors (temperature and salinity) in explaining the changes in chlorophyll-*a*, we compared the observed trends in chlorophyll-*a* with three sets of predictions from model M5: from the full model, from a reduced model formulation with only nutrients as predictors, and from a reduced model formulation with only physical factors as predictors (Fig. 11). We found that only model formulations that included nutrient variables (shown by red and green lines in Fig. 11) were able to explain the high chlorophyll-*a* levels in the 1970s and 1980s, and that physical factors alone could not explain this phenomenon. In contrast, a model with only temperature and salinity (blue lines in Fig. 11) showed similar chlorophyll-*a* levels in the 1970s and 1980s as in later decades. The physical factors mainly contributed to explain the seasonal pattern in chlorophyll-*a* levels, for example the increase from April to May, which was not explainable through nutrients alone (i.e., the nutrients-only model, shown by green lines in Fig. 11, predicted constant chlorophyll-*a* during these months).

## 4. Discussion

Changing from a fjord that was found dirty and unattractive by the general public, the marine pelagic environment of the inner Oslofjorden is believed to have improved significantly during the last thirty years. Data from the monitoring program compiled as far back as 1973 made it possible to study the changes in chlorophyll during this transition period and the possible drivers for these changes. Our analyses revealed that chlorophyll-*a* levels have been significantly reduced during the period 1980 to 1990 and that this reduction is most likely due to a major reduction in the supply of total nitrogen and phosphorus.

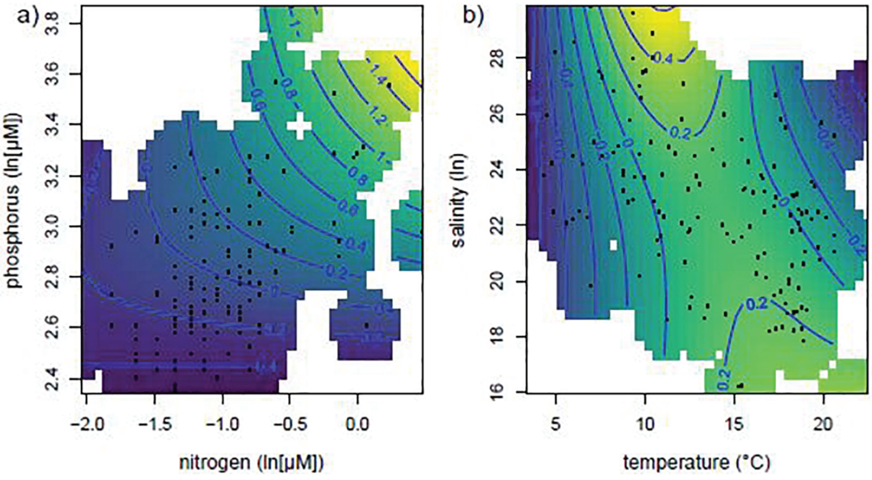

**Fig. 10.** Combined effects of nutrients (a) and temperature and salinity (b) for the levels of chlorophyll-a at DK1 (Steilene) in the inner Oslofjorden estimated by model M5. The plots are from the model with the best AIC and GCV scores, with 37% of variance explained. Chlorophyll-a levels are shown with lighter colours for higher levels. White area is due to a lack of data.

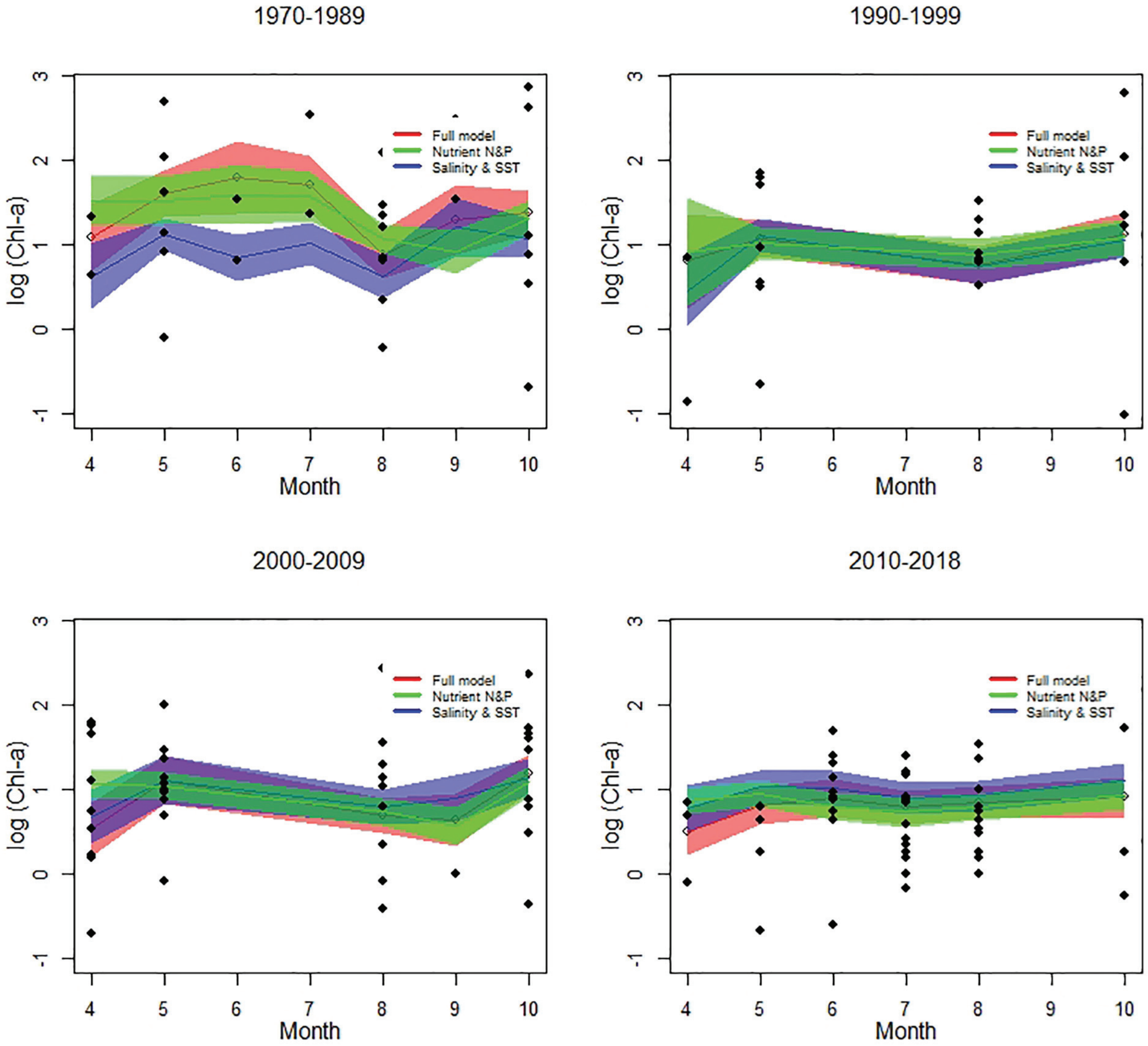

**Fig. 11.** Predictions of chlorophyll-a obtained from model M5 for the five decades covered by the time series. Red colour shows model predictions from the full model, green colour from a model formulation with only nutrients as predictors, and blue colour from a model formulation with only physical factors as predictors. Black points represent observed data from the relevant decade. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### *4.1. Seasonality*

The analyses of seasonal trends showed a strong seasonality in all parameters, as expected at high latitudes (Cloern and Jassby, 2010; Longhurst, 1995). There is a distinct spring bloom in March/April, when light conditions become sufficient, and often an early summer bloom in June and an autumn bloom in September, which is a common pattern in this and nearby areas, like the outer Oslofjorden (Aure et al., 2014; Paasche and Ostergren, 1980) and the Swedish Westcoast (Skjevik et al., 2011).The timing of the two latter blooms are however more variable than the first one. The main changes through the study period were found in the level of the blooms; while before 1990 the chlorophyll-*a* levels could reach 20 μg/L, it has only rarely exceeded 10 μg/L thereafter. Our analyses also indicated that there has been a change towards a later onset of the growth season. This shift is possibly related to increased surface water temperatures (Fig. 7), however, increased temperatures are expected to lead to an earlier onset of the spring bloom (Desmit et al., 2019), while we have seen a possible delay. A prerequisite for the onset of the spring bloom is stratification of the upper water column and our analyses shows a slight seasonal change in salinity, e.g. with the spring decline in salinity occurring later in the year after the 1980s (Fig. 8, Fig. S6)." Salinity generally contributes more than temperature to the stratification in Oslofjorden (Staalstrøm et al., 2012). A delay of the spring bloom could also be related to darkening of coastal waters because of increased amounts of organic matters in the freshwater discharge into the fjords (Opdal et al., 2019). It could also be caused by top-down control by zooplankton (Behrenfeld and Boss, 2014) that hypothetically survive in higher numbers during warm winters.

Our analyses showed a stronger positive correlation of chlorophyll-*a* with phosphorus than with nitrogen in April–May when the chlorophyll-*a* levels are decreasing after the spring bloom and nutrient levels are declining. This finding indicates that year to year trends in chlorophyll-*a* levels at this time of year were best explained by the trends in phosphorus. The concentrations of nutrients (total nitrogen and total phosphorus) decrease through spring and summer to a minimum at the end of August. Our analysis further show a stronger positive correlation of chlorophyll-*a* with nitrogen than phosphorus in June to October, which suggests that year to year trends of the chlorophyll-*a* level at this time of year was best explained by the trends in nitrogen (Fig. 9). One interpretation of these findings is that phosphorus limits phytoplankton growth during spring bloom while nitrogen is limiting late in summer. This was also found in in the western Dutch Wadden Sea (Ly et al., 2014). However, a study from Oslofjorden in 1986 indicated that the summer period was especially phosphorus limited (Paasche and Erga, 1988). Phytoplankton respond to a shortage of phosphate by producing the enzyme alkaline phosphatase, which hydrolyses organic phosphorus into phosphate used for phytoplankton growth. This ability to store organic phosphorus may make the phytoplankton more adaptive to low levels of phosphorus than nitrogen (Lin et al., 2016).

Our analyses are based on total amounts of nitrogen and phosphorus due to limited data of dissolved inorganic nutrients in the long-term dataset. Total N and total P may have limitations in predicting nutrient limitation in autotrophic phytoplankton as they also include biologically unavailable fractions of the nutrients. However, it has been found to perform moderately well with the main shortcoming being high threshold levels (Ptacnik et al., 2010). We therefore conclude that the nutrient-chlorophyll associations found may be underestimated, but significant.

### 4.2. Long term trends

The chlorophyll-*a* levels in inner Oslofjorden decreased by around 70% in the period 1980–1990 (i.e. -1 on the ln scale in Fig. 2), and fluctuated after that, but remained at low levels representing good ecological status. The effects of eutrophication on the phytoplankton community have been documented as far back as the early 1900s (Braarud, 1945; Braarud and Bursa, 1939; Hjort and Gran, 1900; Munthe-Kaas, 1967). Also, the extensive study conducted in 1962–64 documented that the upper water column was heavily eutrofied, and nutrient supply from land-based activities was one of the main sources (Munthe-Kaas, 1968). Our analysis shows that as the levels of chlorophyll-*a* decreased through the 1980s, the Secchi-depth increased. This is an expected relationship, as high biomass of phytoplankton is a major cause of reduced water clarity. However, the trends in Secchi-depth do not follow the trends in chlorophyll exactly. Possible explanations are increased outflow of dissolved organic matter runoff from rivers, which has been found to increase, especially in the eastern part of Norway during the period from 1986 to 2013 (Finstad et al., 2016) and led to darkening of coastal water (Aksnes et al., 2009). This change in turbidity should be studied further in order to determine the impact on primary production and water quality. During the same time as chlorophyll-*a* levels have decreased, the amount of nitrogen in surface water has also decreased steadily and still is. The levels of phosphorus decreased rapidly until around 1998,but have since then increased to the same levels as the beginning of the time series (1973). Model studies from the coastal zone of the North Sea indicate that nutrient loads cannot be linearly correlated to a reduction in primary production (Lenhart et al., 1997). However, it is likely that the reduction of nutrient loads has had an essential impact on the significant chlorophyll-*a* decrease during the study period. Our results further indicate that spring bloom amplitude is controlled by phosphorus. The reduced phosphorus concentration contributed to the decrease in chlorophyll-*a* from 1980s to 1990s. Interestingly, the increase in phosphorus since the 2000s seems not to have led to increased chlorophyll levels, possibly because of limitation from the low nitrogen. This indicates that nitrogen may have become more limiting earlier in the season in later years. To determine whether changes in chlorophyll-*a* level and turbidity are caused by anthropogenic pressures or is natural variability can be especially tricky in temperate fjords with high variation in salinity and temperature (Borja et al., 2016; Elliott and Quintino, 2007). However, in the inner Oslofjorden, the results obtained in this investigation are, to a large extent, coherent with what is expected after a reduction in anthropogenic nutrient load.

### 4.3. Management

The story about the reduced eutrophication and improved water quality of the Oslofjorden is an excellent example of how management initiatives can work and repair some of the old mistakes. The decrease in chlorophyll-*a* levels are likely related to management measures and improved cleaning systems at the sewage treatment plants, especially the introduction of nitrogen removal by biological treatment. The monitoring program was initiated due to concern about the effects of eutrophication of the fjord, but it is now also essential to study the effects of de-eutrophication after cleaning and how other variables such as inorganic particles and dissolved organic matter may affect the pelagic environment. The study station Dk1 in the inner Oslofjorden is not only one of the main stations of the monitoring program, but also a common sampling station included in many research projects in the inner Oslofjorden. Therefore, we managed to fill some of the gaps in the monitoring data with data from other research studies. Even though the main aim of a monitoring program may be the detection of a trend or the non-compliance with a water quality standard (de Jonge et al., 2006), in a rapidly changing environment with new threats and concerns, using monitoring data is essential not only to document the changes but to study how to improve and restore the environment (Cadée and Hegeman, 2002; de Jonge et al., 2006).

The observed improvement in the quality of the surface water through the 1980s (Magnusson et al., 1989; Paasche and Erga, 1988) was assumed to be due to improved sewage cleaning, but based on data available at that time it was not possible to be sure. The observed changes could also be natural fluctuations. Our long-term analysis confirms these early assumptions to be true and shows the long-term significant decrease in chlorophyll-*a* and the close relationship with nutrient levels. However, we also see that after the significant decline, phosphorus has increased since around 1998. We have seen how the reduction in phosphorus has contributed to decrease in the chlorophyll-*a* levels of the spring bloom. As phosphorus levels are increasing again it should be raised as a concern for management. We expect that if the nitrogen levels are kept low, this will most likely keep the chlorophyll levels low too. Due to this situation nitrogen may currently be the critical factor in controlling chlorophyll-*a* phenology in the inner Oslofjorden.

In this study, we have shown how the long-term monitoring dataset from the inner Oslofjorden can be used to understand how anthropogenic pressures contribute to eutrophication and changes in phytoplankton biomass. The analysis here are, however, only indications of biomass changes, and it is also important to understand whether the phytoplankton community composition is changing and how this affects marine biodiversity in the area. There is a growing concern about the local fish stocks in the fjord, as a decrease in the juvenile cod population is evident from the long-term beach seine monitoring (Tore Johannessen pers. com.). In 2019 the Norwegian Directorate of Fisheries closed all fishing of cod (*Gadus morhua*) in the Oslofjorden (Ministry of Trade Industry and Fisheries, 2019). In a rapidly changing environment, with temperature increase, salinity changes, and water darkening, we need this understanding when redesigning monitoring programs to meet future needs and ensure knowledge-based management.

## Declaration of Competing Interest

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.

## Acknowledgement

This work was funded by Fagrådet (for vann og avløpsteknisk samarbeid i indre Oslofjord), the Research Council of Norway (RCN, grant no 262960/O30), and Norconsult. LCS thanks the RCN for support through RCN grant no. 280468. We are grateful to staff at NIVA, especially André Staalstrøm, Jan Magnusson and Guri Sogn Andersen for necessary help to get access to historic monitoring data. We also thank Eivind Aas (UiO) and Svein Kristiansen (UIT) for access to research data. We are also thankful to collages at Norconsult AS and UiO, especially the crew on R/V Trygve Braarud for the collection of more recent data and samples. We also thank Pernille Bechmann for help on digitalizing data from printed reports and Torbjørn Kornstad and Jan David Heuschele for useful input in GAMs and figures.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2020.101925.

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