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Environmental Drivers of Benthic Algal Biomass in the Proximity of Nuclear Power Plants

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Abstract:

Climate change is expected to significantly alter environmental conditions in aquatic ecosystems, for example by increasing water temperatures and acidification through increased heat and greenhouse gas absorption. These kinds of environmental changes can affect primary producers such as benthic algae, which form an important component at the base of food webs. Algae respond rapidly to changes in the environment, so they are widely used as bioindicators of environmental change.

This study examined the effects of water temperature and other environmental drivers on benthic algal biomass in coastal areas near the Loviisa and Olkiluoto nuclear power plants in Finland. Data were analysed using generalized linear models (GLM) to evaluate interactions between environmental variables and benthic algal biomass. The results showed that water temperature and other environmental variables influenced benthic algal biomass, but the effects varied between sites and algal groups. In general, higher biomass values were observed near the power plants' cooling water discharge outlets, although the strength and direction of environmental variables' effects differed between the two study locations and between benthic cyanobacteria, green algae, and diatoms.

The findings indicate that benthic algal biomass responses to different environmental variables are highly context-dependent and cannot be generalized across sites or algal groups. Instead, biomass patterns appear to be driven by environmental factors interacting with each other, rather than a single variable. This highlights the importance of understanding how local environmental conditions as a whole affect benthic algal communities and suggests that future research should focus on interactions between the environmental and site-specific variables when assessing benthic algal responses to power plants' thermal effluent or environmental factors.

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1 Introduction

Climate change is expected to alter environmental conditions globally, as the mean global temperature is predicted to increase 2-4.5°C over the coming century (Masson-Delmotte et al., 2021). Climate change has both direct and indirect effects on aquatic ecosystems. Direct effects include increases in water temperature and acidification, resulting from enhanced absorption of heat and greenhouse gases, especially CO_2, to water. Indirect effects occur through biological interactions, where changes in environmental conditions alter species community composition and abundance. This potentially leads to cascading effects across trophic levels and ultimately affect the ecosystem structure and functioning (Rühland et al., 2015). Both direct and indirect effects of climate change should be studied, as the interplay between these effects can lead to further consequences. These kinds of cascading effects make the primary production at the bottom of the food chains very important. Primary production is the primary energy source and form the foundation of food webs. In aquatic ecosystems, it is formed by algae (Rühland et al., 2015; Winder & Sommer, 2012). Algae, comprised of both microscopic organisms as well as larger macrophytes, respond quickly to changes in the environment, which makes them excellent to monitor changes in environmental conditions (McCormick & Cairns, 1994). In aquatic ecosystems, one key components of primary production are benthic algae (periphyton), which are the focus in this study.

The understanding of long-term effect of climate change and warming of oceans, lakes and other water bodies requires extended study periods, thus making the effects difficult to predict. However, sites with localized warming – such as those near geyser basins (Boylen & Brock, 1973), experimentally heated chambers (Sapucaia et al., 2024) and the thermal effluent of power plants (Begun & Maslennikov, 2021; Du et al., 2026; Ilus & Keskitalo, 2008; Széchy et al., 2017) provide opportunities to study these effects on benthic algae on a smaller spatial and temporal scale. Previous studies show that changes in environmental factors, such as water temperature, nutrient concentrations, water acidity, and current, can directly and indirectly affect benthic algae (McCormick & Cairns, 1994; Pniewski & Sylwestrzak, 2018; Sapucaia et al., 2024). The topic has been studied previously in multiple different locations, settings, and environmental conditions.

However, many previous studies such as those by Begun and Maslennikov (2021), and Ilus and Keskitalo (2008) have largely focused on phytoplankton, while benthic algae have

received considerably less attention. In particular, there is still limited understanding of how different environmental variables, especially water temperature, individually influence the biomass of benthic algal groups in varying environments. In addition, the relative importance of water temperature compared to other environmental drivers remains unclear across different study settings, and with projected climate change scenarios, it is likely to be a central variable in the future. This study addresses these gaps by examining the effects of water temperature, along with other environmental variables, on benthic algal biomass in the proximity of two nuclear power plants in Finland at the Baltic Sea coast. By focusing on benthic algae, this study provides an additional perspective to existing phytoplankton-centred research and aims to improve understanding of how local environmental conditions shape algal community responses to varying thermal conditions. At the same time, this study acknowledges that ecosystem responses are highly context-dependent, and the results should therefore be interpreted as one contribution to a broader field of research, rather than broadly general information or widely applicable solutions.

This thesis aims to (1) investigate how water temperature affects benthic algal biomass near nuclear power plants in Loviisa and Olkiluoto (the effect of thermal effluent), and (2) investigate the influence of water pH, conductivity, and total phosphorus and nitrogen concentrations on benthic algal biomass. It further aims to (3) examine whether benthic cyanobacteria, green algae, and diatoms respond differently to thermal effluent and the other environmental factors. In addition, by using two study locations with different temporal frequency of sampling, this study considers whether the research questions can be addressed using a sparser sampling method, or whether a more intensive sampling approach is necessary.

2 Theoretical background

2.1 The role of benthic algae in aquatic ecosystems

Benthic algae are photosynthetic organisms that live attached to submerged surfaces like rocks, sediments, and vegetation in aquatic ecosystems (Sapucaia et al., 2024). They form an important part of primary production in both freshwater and marine environments and contribute significantly to nutrient cycling, oxygen production, and aquatic food webs (Rühland et al., 2015; Winder & Sommer, 2012). Through photosynthesis, benthic algae provide energy for higher trophic levels and support aquatic ecosystem productivity.

Benthic algae consist of several taxonomic groups with different physiological and ecological traits. Among the most common groups are cyanobacteria, green algae, and diatoms, and although these groups share the ability to photosynthesize, they differ in their responses to environmental variability. As Winder & Sommer (2012) state, environmental conditions can alter benthic algal community composition by favouring some taxa while disadvantaging others. Furthermore, changes in benthic algal communities extend beyond the algal layer itself and affect higher trophic levels, influencing the functioning of the entire aquatic ecosystem (Shurin et al., 2012). Benthic algae, and especially benthic diatoms, are also widely used as bioindicators of environmental change (McCormick & Cairns, 1994). As many taxa respond rapidly to changes in water chemistry, nutrient concentrations and temperature, benthic algal communities can reflect variation in aquatic ecosystems from both natural and human influenced processes.

2.2 Environmental drivers of benthic algae biomass

2.2.1 Light

Light is the primary energy source for photosynthesis and therefore a key factor affecting the growth of benthic algae (Hill et al., 2001; Schiller et al., 2007; Singh & Singh, 2015). Because benthic algae rely on photosynthesis for energy production, reduced light availability can directly limit biomass growth. Even when other environmental requirements such as nutrient concentrations are sufficient, low light availability can restrict primary production and biomass growth (Schiller et al., 2007). The amount of light reaching the benthic layer depends on several factors, including seasonality, water depth, turbidity, shading, and water movement. Both spatial and temporal variation in light

availability can have major effect on benthic algae, especially in high-latitude environments where seasonal light availability is generally already lower. For example, Rühland et al. (2015) showed that longer ice cover duration can significantly reduce primary production during winter and spring, as the ice layer blocks incoming solar rays. Similarly, springtime flooding can increase water turbidity, and as turbid or brown-coloured water reduces light availability due to suspended particles and dissolved organic matter absorbing light, restrict the amount of light reaching the benthic layer (Singh & Singh, 2015). In deeper waters, light availability decreases even further due to increased absorption, reflection, and refraction in the water layer.

Different benthic algal groups also respond differently to light conditions, which may influence community composition under changing environmental conditions. Benthic green algae often respond rapidly to high light availability in shallow, nutrient-rich waters due to their fast growth rates (Singh & Singh, 2015). In contrast, high phytoplankton biomass may reduce light penetration and benthic algal biomass growth through shading effects (Mahdy et al., 2015). Schiller et al. (2007) further identified light availability as one of the main factors controlling benthic algal biomass in stream ecosystems, highlighting its importance.

2.2.2 Water temperature

Water temperature is one of the key environmental factors affecting benthic algae biomass (Mahdy et al., 2015). Temperature affects fundamental physiological processes, including nutrient and CO_2 uptake, photosynthesis, enzyme activity, and cellular composition (Mei et al., 2022; Singh & Singh, 2015). Because metabolic processes are dependent on water temperature, warmer conditions can increase algal growth and photosynthetic activity up to a certain threshold. Beyond this threshold, however, respiration and cellular stress may increase faster than photosynthesis, which leads to reduced biomass and changes in the community composition.

The relationship between temperature and algae growth, therefor, is non-linear. Each algae taxa has an optimal temperature range for maximum growth (Bécares et al., 2008; Hansson, 1992; Priddle et al., 1986). Consequently, both low and high temperatures can limit algae biomass, although these limits vary depending on other environmental conditions such as nutrient and light availability, as well as the composition of the benthic algal community itself.

Thus, because different algal taxa have different optimum temperature ranges, changes in water temperature can alter community composition and favour other species while disadvantaging others. Cyanobacteria, for example, often benefit from elevated temperatures and may form harmful algal blooms under warm conditions (Paerl et al., 2011). In contrast, benthic diatom assemblages are often highly sensitive to temperature changes, which can cause them to become smaller in size reducing the biomass, and lower the species richness in the habitat (Svensson et al., 2024; Virta & Hedberg, 2024). Changes in temperature may also affect the competition between benthic algae and phytoplankton, which can lead to negative effects on water quality, and which then again indirectly affects benthic algae (Mei et al., 2022).

While temperature is a key environmental factor in aquatic ecosystems, the effects of temperature on benthic algae are not consistent across studies. Some research has shown increases in benthic algae biomass with increased water temperatures (Patrick et al., 2012), while others suggest declines in benthic algae chlorophyll-a and, consequently, the biomass, with similar water temperature changes in different ecosystems (Shurin et al., 2024). Also, findings by Hansson (1992) further suggest that low water temperature does not consistently limit benthic algal biomass growth, but rather that the effect largely depends on the environment. Mahdy et al. (2015) also suggest that these variations may result from temperature interactions with other environmental factors, such as nutrition and light availability, competition for resources with phytoplankton, and grazing pressure by invertebrates. Because of this, the effects of water temperature on benthic algae are difficult to estimate and create complicated interactions between various environmental variables.

2.2.3 Nutrient availability

Nutrient availability is another central factor to benthic algal biomass. In many aquatic systems, total nitrogen and phosphorus concentration are the primary limiting nutrients for algal biomass (Schiller et al., 2007). As algae are the base of aquatic food webs, their interactions with nutrients affect the higher trophic levels as well and contribute to nutrients moving up trophic levels.

Nutrient concentrations affect algae photosynthetic rates, enzyme activity and the biochemical composition of algal cells (McCormick & Cairns, 1994; Schiller et al., 2007). With enough nutrients, algae growth and chlorophyll-a production is generally promoted.

When nutrients are limited, the growth typically slows down. However, if nutrient concentrations become very high while nutrient availability would otherwise be a limiting factor, algae can grow excessively and limit oxygen levels in water as the algae die and begin to decompose. Excessive algae growth and decomposition caused by increased nutrient loading can lead to depletion of oxygen concentrations in the water body, a process known as hypoxia (McCormick & Cairns, 1994). If oxygen levels continue to drop, hypoxia can escalate into anoxia, or the complete absence of oxygen in water. Such conditions disrupt aquatic life and promote eutrophication.

Different algae groups respond differently to nutrient availability. Green algae often dominate under nutrient-rich conditions due to their fast growth and efficient nutrient uptake mechanisms (Salo & Salovius-Laurén, 2022). Diatoms typically thrive under moderate to high nitrogen and phosphorus concentrations (Alipanah et al., 2018). Cyanobacteria, in contrast, may gain an advantage in low-nutrient environments due to their ability to fix nitrogen, thereby outperforming other algal groups under certain environmental conditions (Paerl et al., 2011). However, studies also show that cyanobacteria often thrive in nutrient-rich conditions (Lürling et al., 2018), which demonstrates their adaptability to various environmental conditions. When nutrient availability favours certain algal groups or taxa over others, community composition may shift, potentially leading to reduced biodiversity across trophic levels. Paerl et al. (2011) further emphasize the role of cyanobacteria, as projected climate change conditions may enhance their competitive advantage, leading to more harmful algal blooms.

2.2.4 Water pH and conductivity

While water temperature and nutrient availability are often emphasized in literature as major factors in algae growth, other aspects of water chemistry also play a significant role. Water pH and conductivity are two factors inspected in this work. Water pH determines how acidic or alkaline the water is, while conductivity is used as an indirect indicator of dissolved ions concentrations. These factors affect how nutrients are taken up and how efficiently benthic algae can carry out photosynthesis, therefore contributing to biomass growth.

Water pH affects enzyme activity, nutrient availability and overall metabolism in benthic algae (Roleda et al., 2015). Changes in pH-levels can alter the algal community composition. Very acidic water can disrupt the structure of algae cells and reduce

photosynthetic efficiency, leading to lower species diversity and productivity in the habitat (Eloranta et al., 2007). Water acidification may also alter the community structure by favouring taxa more resistant to lower pH-levels while excluding more sensitive species (Roleda et al., 2015). In contrast, neutral to slightly alkaline waters generally support a greater diversity of benthic algae and higher rates of primary production (Eloranta et al., 2007). Some taxa, such as certain diatoms and cyanobacteria, can tolerate a wider range of pH conditions, allowing them to be successful in environments that would otherwise be less favourable for most other species (Rodríguez-Miret et al., 2025; Zhang et al., 2024).

Conductivity describes the ability of water to conduct an electrical current, which depends on the concentration of dissolved ions such as minerals and salts. In aquatic ecosystems, it is often used as an indirect indicator of nutrient availability (Sapucaia et al., 2024). Moderate conductivity levels can enhance nutrient transport and availability, which may promote algal growth. On the other hand, too high conductivity can indicate pollution or eutrophication, which can cause stress and reduce biodiversity. Conductivity often correlates with nutrient enrichment, so it is sometimes used as an indicator of eutrophication and the influence of land use or anthropogenic stress inputs. Monitoring conductivity can therefore provide useful information on the chemical environment and the condition of the habitat.

2.2.5 Other factors

Water flow is especially important for benthic algae in stream environments, as it affects nutrient delivery, gas exchange, and the removal of organic matter from surfaces (Eloranta et al., 2007). According to Eloranta et al. (2007), moderate water movement generally supports algae growth by improving the supply of oxygen and nutrients. However, if flow rates become excessively strong, algae can be physically removed from the substrate they are attached to, reducing biomass and potentially changing the community composition as well. On the contrary, very low flow conditions may limit oxygen availability and nutrient transport, leading to stress and reduced productivity.

Benthic algae also interact closely with phytoplankton, which occupy the same aquatic environment but live freely in the water column rather than attached to surfaces. Because both groups require similar resources, the primary competition between the groups is for light and nutrients. High phytoplankton biomass can reduce light availability in the water column through shading, thus limiting benthic algal growth (Mahdy et al., 2015). Water

temperature may further influence this balance, as elevated water temperatures often favour phytoplankton over benthic algae. This shift in balance can lead to effects on the whole aquatic ecosystem, such as reduced oxygen production in benthic layer and increased risk of hypoxia and anoxia due to benthic decomposition (Mei et al., 2022). The dominance of either group is strongly dependent on environmental conditions. Phytoplankton typically dominate in deeper or more nutrient-rich waters where light availability is strongly limited in the bottom, whereas benthic algae are more successful in shallow systems with lower nutrient concentrations, where light availability is better and access to sediment nutrients provides a competitive advantage (Sand-Jensen & Borum, 1991).

Besides phytoplankton, benthic algae are affected by grazing organisms living in the benthic layer. The benthos, which means all the plants and animals living closely associated with the bottom of a water body, includes for example snails, insect larvae, and some fish species. They regulate algae biomass and affect species community composition through grazing pressure (Hillebrand & Kahlert, 2001), but not necessarily negatively by grazing the benthic algae itself. In fact, Hillebrand & Kahlert (2001) suggest that moderate grazing pressure can promote diversity and biomass accumulation by removing deteriorating cells or shading macrophytes, increasing excretion of nutrients or increasing nutrient uptake, although excessive grazing may significantly reduce algae biomass.

Finally, land use within the catchment area can indirectly shape many of the environmental factors affecting benthic algae. Agriculture and urban land use in catchment area often increase nutrient and sediment loading, resulting in increases turbidity and altered conductivity and pH conditions (Camara et al., 2019). In contrast, forested catchments often have lower nutrient concentrations but may cause brownification through the input of dissolved organic carbon. Land use may additionally influence the pollutant concentrations, including heavy metals and organic contaminants, which can have toxic effects on benthic algae, reduce productivity, and modify community composition (Camara et al., 2019). Additionally, land use can cause chances in water flow, which can create indirect effects on benthic algae.

2.3 Processes in the hydrology of nuclear power plants

Looking at environmental factors like water temperature, and nutrient availability is one side of studying aquatic ecosystems, but another important side is human influence. A

number of human activities have direct and indirect effects on water quality, of which energy and electricity production are one of the most influential (Leng et al., 2024). Water is important for both nuclear and thermal power plants, as they rely heavily on it for cooling purposes. Massive amounts of water are moved through the power plant's cooling system, where they remove excess heat from the reactor or steam turbines before being discharged back into the surrounding environment (Leng et al., 2024). This can have various effects on the surrounding aquatic environment, from the excess heat load to changes in water chemistry, to various effects to phytoplankton and fish that are drawn in with the cooling water (Ilus & Keskitalo, 2008; Mahnala, 2024). The way the cooling process is carried out technologically varies between facilities and depends largely on the type of cooling system employed. In general, power plants use one of two main approaches: once-through cooling or closed-cycle cooling, each with their own outcome for water use and environmental impact.

In once-through systems, water is withdrawn directly from a nearby natural source, like a river, a lake or a coastal area, and passed through the system's heat exchangers where it absorbs excess heat. Finally, it is discharged back to the source at a higher temperature (Madden et al., 2013). These systems are efficient in terms of cooling capacity but result in very large volumes of warm water being released, often causing significant localized thermal changes. On the other hand, closed-cycle systems, or recircling systems, use cooling towers or ponds to move heat before reusing the same water in the system. While these systems withdraw much less water, they can still lead to some thermal and evaporative effects, although smaller in spatial extent than those of once-through systems (Khamis & Kavvadias, 2012). They also require much more investments and operating costs. The geographical location of the power plant and the available funding are two major factors to determine which system is used.

When heated water from a power plant is released into a natural body of water, it creates localized temperature anomalies often referred to thermal effluent, which can alter the physical, chemical and biological properties of the receiving environment (Madden et al., 2013; Wang et al., 2025). For physical properties, elevated water temperature affects water stratification by adding vertical mixing. Warmer, less dense water tends to remain on the surface, which can reduce oxygen exchange between different layers in water and influence flow dynamics. Reduced mixing may lead to lower oxygen concentrations in deeper waters and change the transport of nutrients and suspended materials (Leng et al., 2024). For

chemical and biological properties, higher temperatures accelerate metabolic and biochemical processes, influencing respiration, decomposition, and nutrient cycling, as explained in section 2.2.2. These changes can indirectly affect different aquatic organisms, including benthic algae and the entire benthos, which are sensitive to shifts in temperature, light availability and oxygen levels (Leng et al., 2024; Wang et al., 2025). Elevated temperatures may also intensify phytoplankton growth, increasing competition for light and nutrients (Peeters et al., 2007).

The hydrological processes involved with cooling water in power plants' thermal effluent create small, localized conditions that can be used as case studies for studying the ecological effects of water temperature variation. The presence of a localized heat source makes it possible to observe how temperature influences aquatic communities, under relatively controlled conditions. For benthic algae, these kinds of environments provide opportunities to investigate how long-term exposure to elevated water temperatures affects growth, community composition and interactions with other environmental factors such as nutrients and light. Long-term before-and-after studies done on power plant sites show that the added water temperature will change the species composition around the site (Ilus & Keskitalo, 2008; Schiel et al., 2004). However, because the thermal discharge from a power plant is relatively steady, it can be difficult to identify and interpret the effects of temperature and its interactions with other factors after the power plant is active. As a result, Ilus and Keskitalo (2008) found in their study that it is also possible for the relative importance of environmental variables on the aquatic environment to change significantly due to the thermal effluent.

3 Research area

3.1 Loviisa

The Loviisa nuclear power plant is located on the island of Hästholmen in the municipality of Loviisa on the southern coast of Finland (Figure 1). The power plant consists of two pressurized water reactors (PWRs), Loviisa 1 and Loviisa 2, which began operation in 1977 and 1980 (Fortum, 2025). Both reactors use once-through cooling systems, where seawater is taken from the western side of the island from Hudöfjärden and discharged to the eastern side into Hästholmsfjärden. During the cooling process, the temperature of the water increases by approximately 10 °C before being returned to the surrounding coastal area.

The six sampling sites in Loviisa are Hästholmen west, Hästholmen east, Fish farms, Ryssviken, Jomalsund, and Bölsviken. Hästholmen east and Fish farms are located near the cooling water discharge area, whereas Hästholmen west is situated near the cooling water intake channel, as seen in Figure 1. Ryssviken, Jomalsund, and Bölsviken were located further from the power plant area. Environmentally, all the sites are affected by the brackish conditions of the Baltic Sea. However, due to differences in the proximity to the cooling water discharge outlet, freshwater influence, and other local environmental conditions, the sampling sites represent environmentally diverse habitats. For example, some sites located further from the power plant, especially Jomalsund, are potentially affected by freshwater inflow from the Kymijoki river, which flows to the coast in the northern part of the study area. Freshwater inflow may affect conductivity, nutrient concentrations, and overall water chemistry. Additionally, Bölsviken is located in a small bay and compared to the other sites, the area around the site has more abundant aquatic vegetation.

Figure 1. Location of the sampling sites in Loviisa, with the inset map showing the study location in Finland. The stars indicate the nuclear power plant cooling water intake channel (1) and discharge outlet (2). Hästholmen west, Hästholmen east, and the Fish farm site are located in closer proximity to the nuclear power plant, while Bölsviken, Jomalsund, and Ryssviken are further away. One of the inflow locations for the Kymijoki river can also be found in the northern part of the study area, near Jomalsund. Basemap: OpenStreetMap 2026.

3.2 Olkiluoto

The Olkiluoto nuclear power plant is located on the island of Olkiluoto in the municipality of Eurajoki on the western coast of Finland (Figure 2). The power plant consists of three reactors: Olkiluoto 1 and Olkiluoto 2, which began operation in 1978 and 1980, respectively, and Olkiluoto 3, which began operation in 2023 (TVO, 2023, 2026). Olkiluoto 1 and 2 are boiling water reactors (BWRs), while Olkiluoto 3 is a pressurised water reactor (PWR). Similarly to Loviisa nuclear power plant, all three reactors use once-through cooling systems. In Olkiluoto, seawater is taken from the eastern side of the island from Olkiluodonvesi and discharged to the western side into Iso Kaalonperä. Unlike in Loviisa, Olkiluoto has two separate cooling water intake channels: one shared by Olkiluoto 1 and 2, and another for Olkiluoto 3. This arrangement is related to differences in reactor design and cooling water requirements between the units.

The six sampling sites in Olkiluoto are Visiting centre, Olkiluoto east, Olkiluoto west, Kuusisenmaa, Munakari, and Tankarit. Visiting centre and Olkiluoto east are located near the cooling water intake channels, while Olkiluoto west and Kuusisenmaa are near the discharge outlet. Munakari and Tankarit are further away from the power plant and possibly represent slightly different environmental conditions of the Eurajoensalmi strait. Similarly to Loviisa, Olkiluoto area also has freshwater inflow from a river, as the Eurajoki river flows to the sea in the east of Tankarit.

Figure 2. The location of the sampling sites in Olkiluoto, with the inset map showing the study location in Finland. The stars indicate the nuclear power plant's cooling water intake discharge outlet (1), Olkiluoto 3 reactor's (2) and Olkiluoto 1 & 2 reactors' intake channel (3). Olkiluoto west, and Olkiluoto east are in closer proximity to the discharge outlet, while Visiting centre is near the intake channels. Munakari and Tankarit are located further away from both the intake channels and the discharge outlet. One of the inflow points of the Eurajoki river is located to the east of Tankarit. Basemap: OpenStreetMap 2026

4 Material and methods

4.1 Field work

The sampling sites for field work in both study locations were chosen together with experts from Fortum Oyj and TVO Oyj, as well as the supervisor of the thesis. The sites were chosen with consideration put to which areas could possibly be affected by the nuclear power plants' thermal effluent. On top of this, accessibility was also considered, as all the sites at the locations had to be visited in a day when taking samples to ensure similar weather conditions between the sites for comparability. The sites were not visited beforehand, which meant that the exact sites changed slightly during the first sampling day, to account accessibility.

Field work was done between late May and mid-October of 2025. The primary study location, Loviisa, was visited 12 times. The initial goal was to visit the sites there every two weeks to align with benthic algae life cycles and capture the change in water quality. This goal was largely met, with sampling done every 10–14 days to accommodate for weekend site access restrictions and personal scheduling. Sites in Loviisa were consistently visited in the same order during each sampling day to maintain consistency. The secondary study location, Olkiluoto, was visited three times in total to capture conditions at the beginning, middle and end of the sampling period. At this location, the order of site visits was slightly modified after the first visit to optimise daily efficiency.

At each site, benthic algal biomass (µg chl-a/cm^2) was measured using a BenthoTorch device (Figure 3). BenthoTorch uses the *in vivo* fluorescence of algal cells to calculate the different algae as chlorophyll-a concentrations, and then internally calculates the biomass counts (BenthoTorch - Bbe Moldaenke, 2025). Using mean values of multiple measurements has been used in previous studies with, for example, benthic diatom sampling (Eloranta et al., 2007), and the same methodology was used for this study. Underwater rock surfaces near the shore were measured a total of ten times per site. The rocks were chosen randomly, however, avoiding any surfaces with visible macroalgae, as it can interfere with BenthoTorch measurements of the fluorescence of benthic algae. In addition, the physicochemical properties of the water were measured using a YSI measurement tool (Figure 4). The device was submerged for five minutes at each site to take readings for water temperature (°C), water pH and conductivity (µS/cm). The YSI device was calibrated for pH before each field day by conducting a three-point calibration

with standard buffer solutions. Other sensors in the device were calibrated by laboratory staff at Kumpula Campus. Finally, a 250 ml water sample was collected at each site for total nitrogen (TN) and total phosphorus (TP) concentration analysis. Data were initially recorded on paper field forms in-situ and later taken into Microsoft Excel. Additionally, a picture was taken at every site (Appendix 1).

Figure 3. BenthoTorch device used for the benthic algal biomass measurements.

Figure 4. YSI device used to measure the physiochemical properties of water.

Due to significant fluctuations in water levels observed during the sampling period, additional water level data (N2000) were obtained from the Finnish Meteorological Institute (Finnish Meteorological Institute, 2025). Data from the Porvoo station were used for Loviisa, while data from Rauma were used for Olkiluoto.

4.2 Laboratory work

The laboratory work was done in multiple set over the course of summer and autumn of 2025 due to the large number of samples. The samples were kept in a cooler (approx. 4°C) until the laboratory work was done. All the analyses were done at the Department of Geosciences and Geography laboratories at the Kumpula Campus, Helsinki University.

The oxidation in the total nitrogen analysis was done based on standard SFS-EN ISO 11905-1, and the measurement of total nitrogen was based on the “Standard Methods for the examination of water and wastewater” method 4500-NO3- B Ultraviolet Spectrophotometric screening. Nitrogen compounds in the samples were oxidized to nitrate using peroxysulfate and high temperature and pressure. The absorbance of nitrate

was measured with a spectrometer at a wavelength of 220 nm and the absorbance of the interfering dissolved organic matter at a wavelength of 275 nm. Total phosphorus analysis was done based on standard SFS-EN ISO 6878. Phosphorus compounds in the samples were oxidized to orthophosphate ions using potassium peroxodisulfate and high temperature and pressure. An acidic solution was added to form phosphomolybdate, whose absorbance was measured with a spectrometer at a wavelength of 880 nm to determine total phosphorus concentration. To ensure the reliability of the analysis, zero, control, and replicate samples were included in all sets of laboratory work.

4.3 Statistical analysis

Initial data processing was performed in Microsoft Excel. For each sample, mean algal biomass was calculated from the ten replicate measurements. Four observations with zero biomass were adjusted to a small positive value (0.001) to enable the use of gamma distributions, which require strictly positive response values. All statistical analyses were done in RStudio (version 4.4.1). Linear and generalized linear models were fitted using the base R *stats* package, while mixed-effects models were fitted using the *lme4* package. The *ggplot2* package was used for data visualization and plotting. The response variables included total algal biomass as well as biomass of cyanobacteria, green algae and diatoms. Predictor variables included water temperature, pH, conductivity, total nitrogen (TN), total phosphorus (TP) concentrations, water level, and sampling day.

Before modelling, multicollinearity between predictor variables was assessed using Spearman's correlation analysis (Appendix 2). In the dataset for Olkiluoto, strong correlation ($\rho > 0.70$) was observed between conductivity, water level median and sampling day, and the relationships between these variables were considered during model creation and interpretation. However, full models containing all environmental variables were kept for the final analyses to maintain a consistent model structure between the two study locations and all algae groups. This allowed more direct comparison between datasets and intensive and sparse sampling approaches at the different locations. Having the same predictor variables across all models was also considered from an ecological view, as benthic algal biomass is likely influenced by interactions between multiple environmental factors rather than by single variables independently, so leaving out non-significant variables from the models could affect interpretations of the results. Conductivity values were log-transformed due to their substantially larger magnitude

compared to the other environmental variables. In addition, all predictor variables were standardized using the scale() function in base R to improve numerical stability and enable comparison between model coefficients.

Several model structures were evaluated during the analysis process, including linear models (LM), linear mixed-effects models (LMM), generalized linear mixed-effects models (GLMM) and generalized linear models (GLM). Random effects from site grouping were assessed in the mixed-effects models. However, in most cases there was not enough estimated variance in the random effect, indicating the sites were too similar, and thus mixed effects models were not used in the final analyses. Diagnostic checks for linear models indicated violations of model assumptions, including heteroskedasticity and non-normal residual distributions. Because biomass data were strongly right skewed and strictly positive, GLM with gamma distribution was considered most appropriate for the analyses. The full generalized linear models generally showed improved model fit based on Akaike Information Criterion (AIC) values and explained deviance compared to reduced models with fewer predictor variables, or other evaluated model structures. Therefore, generalized linear models with gamma distributions were selected for the final analyses.

5 Results

5.1 Loviisa

5.1.1 Environmental variables

Water temperatures in Loviisa followed a general seasonal trend from early summer to autumn, though spatial variation was evident between sampling sites. The highest temperature (+33°C) was recorded on July 29th at Hästholmen east (Figure 5), which is located near the cooling water discharge outlet. For comparison, the opposite side of the island (Hästholmen west) reached only +25.9°C on the same day. Temperatures reached their minimum during the final sampling in October, with the lowest value (+11.9°C) measured at Jomalsund. While the temporal trend was similar across all sites, Hästholmen east remained consistently warmer, with temperatures exceeding +18°C throughout the sampling period. One exception to the temporal variation occurred in mid-September, when temperatures briefly peaked before continuing to drop. As a note for the results, it should be noted that the lines in the figures serve only to connect individual observations and do not represent the actual variation in data between sampling dates.

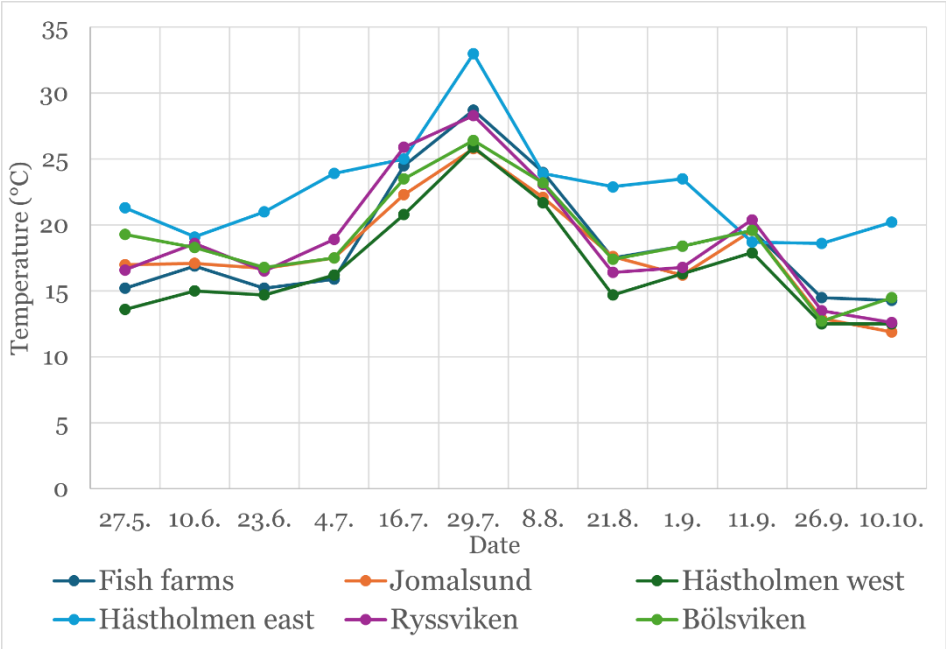

Figure 5. Variation in water temperature at the sampling sites in Loviisa during the summer and early autumn of 2025.

The pH levels across the study sites spanned from 6.5 to 9.8, indicating a moderately wide range with a notably high maximum value. Despite this, the mean and median were both

8.1, suggesting a symmetric distribution with no significant skew. Half of the measurements fell between 7.7 and 8.6, which points toward generally alkaline conditions throughout the sampling period. The variation in pH was more complex between the sites than what was observed for water temperature (Figure 6). This was particularly evident during the sampling days in August, where the sites split into two different patterns: Fish farms, Hästholmen west, and Hästholmen east showed lower pH-levels than in previous sampling times, whereas Jomalsund, Ryssviken and Bölsviken showed a clear increase. These groups showed similarities in pH-levels during the sampling period overall. For instance, Bölsviken and Ryssviken followed nearly identical variation across the entire sampling period, most notably in the heavy variation between July 4th and July 29th, where pH remained relatively stable at all other sites. When interpreting the results, it should be noted that that the pH values of 21st of August are imputed from the following measurements dues to missing values. This is discussed in later sections.

Water conductivity ranged from 373 to 9153 µS/cm in Loviisa. The middle 50% of the measurements were between 7018 and 8332 µS/cm, with the median (7946 µS/cm) and mean (7388 µS/cm) values being relatively close to each other. While most sites displayed similar and rather modest temporal variation in conductivity levels, Jomalsund emerged as a significant outlier (Figure 7). While all other sites remained above 6476 µS/cm during the entire sampling period, the values at Jomalsund fluctuated between 373 and 7395 µS/cm, and had a much lower median (5297 µS/cm) and mean (3297 µS/cm) values compared to the rest of the sites. However, despite these overall lower values, the temporal variation at Jomalsund was similar to the trends seen at the other sites. Aside from this, Hästholmen east showed a slight deviation from the other sites with higher peaks on the 8th of August and the 26th of September.

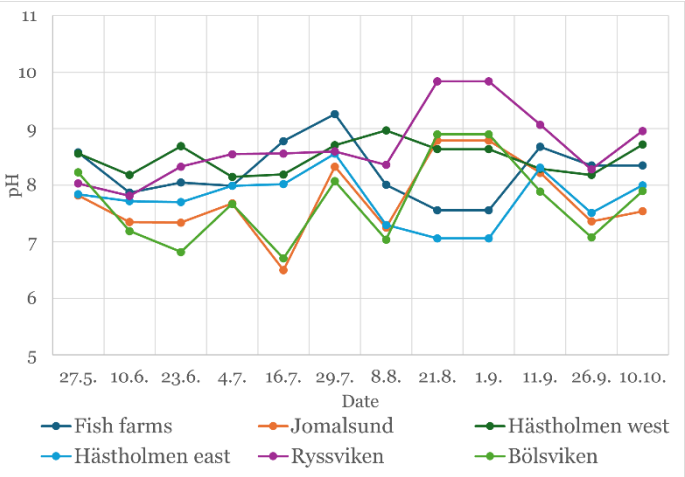

Figure 6. Variation in water pH levels at the sampling sites in Loviisa during the sampling period.

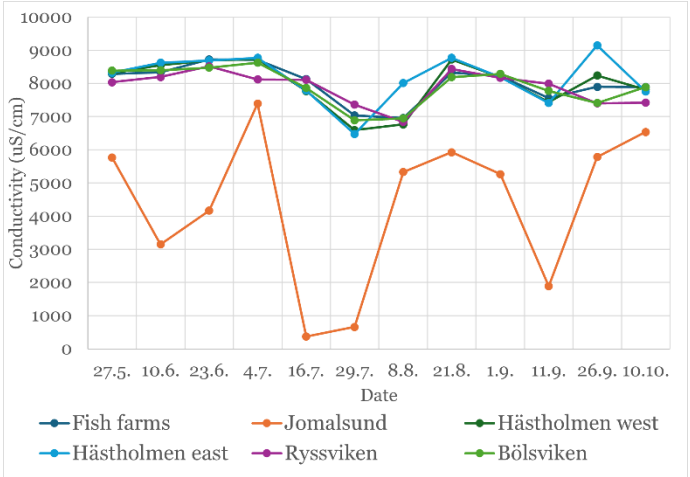

Figure 7. Variation in water conductivity (µS/cm) at the sampling sites in Loviisa during the sampling period.

Total nitrogen (TN) had a mean concentration of 0.797 mg/l and a median concentration of 0.650 mg/l. The lower quartile was 0.563 mg/l, and the higher quartile was 0.725 mg/l. While concentrations remained generally stable throughout the sampling period, some short-term fluctuations were observed, as for example Jomalsund and Fish farms showed peaks of 1.825 mg/l and 1.463 mg/l on the 16th of July (Figure 8). The highest TN concentrations were measured on the final sampling day in October, at Bölsviken (5.2 mg/l) and Ryssviken (3.263 mg/l), while other sites remained at lower TN concentrations.

Total phosphorus (TP) had a mean concentration of 69.2 µg/l, and a median concentration of 40.1 µg/l. The lower quartile was 34.9 µg/l, and the higher quartile was 53.1 µg/l, which compared to the TN concentrations along with a strong positive Spearman correlation (ρ = 0.64), suggests similarities in variation between the nutrients. TP concentrations stayed moderately stable and showed only two significant changes: increases in Jomalsund on the 16th of July, and in Ryssviken and Bölsviken on the final sampling day on the 10th of October (Figure 9). Similarly to TN, TP concentration had a significantly high maximum value of 945 µg/l, which was also measured on the same sampling day at the end of the sampling period.

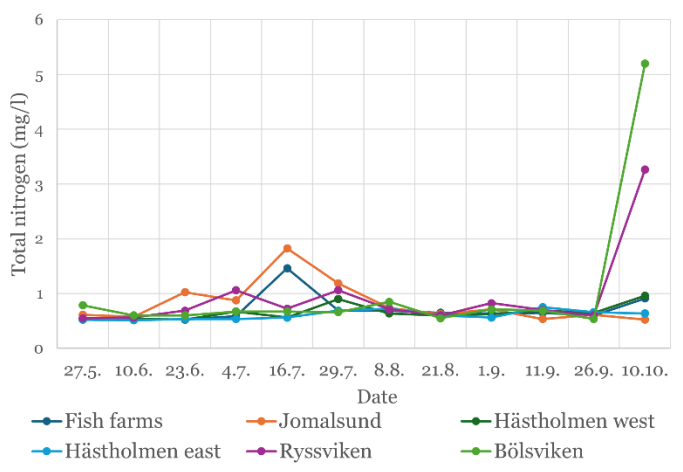

Figure 8. Total nitrogen (mg/l) at each site in Loviisa during the sampling period.

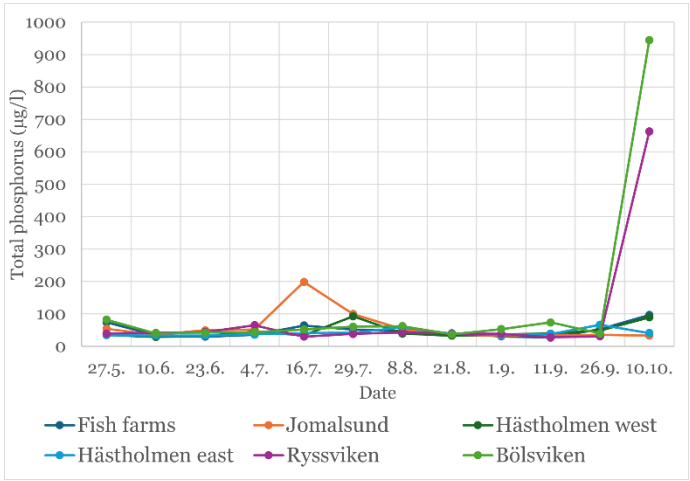

Figure 9. Total phosphorus (µg/l) at each site in Loviisa during the sampling period.

5.1.2 Benthic algal biomass

Algal biomass composition across the six sampling sites in Loviisa was characterized by a dominance of cyanobacteria and diatoms, while green algae consistently represented only a small part (Figure 10). Cyanobacteria biomass remained moderately similar at most sites, with median values ranging from 0.6 to 1.8 µg chl-a/cm². The highest median cyanobacteria biomass was measured at Bölsviken, which also showed the greatest temporal variability in cyanobacteria biomass and differed from the other sites where in contrast, cyanobacteria biomass levels were notably lower and more uniform. Diatoms showed greater variability across all sites, with median values ranging from 0.5 to 2.1 µg chl-a/cm². Highest median values were measured at Bölsviken and Hästholmen east, where median values were just over 2 µg chl-a/cm². At other sites, diatom biomass distribution was characterized by low median values but long whiskers and multiple exceptional outliers indicating that there is a strong temporal variation in biomass. Green algae biomass remained low across all sites. Especially Fish farms stood out from the rest of the sites in green algae biomass, as the median value of 0.1 µg chl-a/cm², was very close to the lower quartile value of 0.07 µg chl-a/cm², indicated by the closeness of the box border and the median line. This suggests that green algae biomass data was very skewed at Fish farms. Similar skewedness can also be found at Bölsviken, Ryssviken, and Hästholmen east. While green algae had some outliers at half of all the sites, they remained inside cyanobacteria or diatom ranges, with green algae as the smallest group at all sites.

In total, four measurements located at different sites resulted in zero green algae biomass, which could be the result of either equipment or environmental conditions.

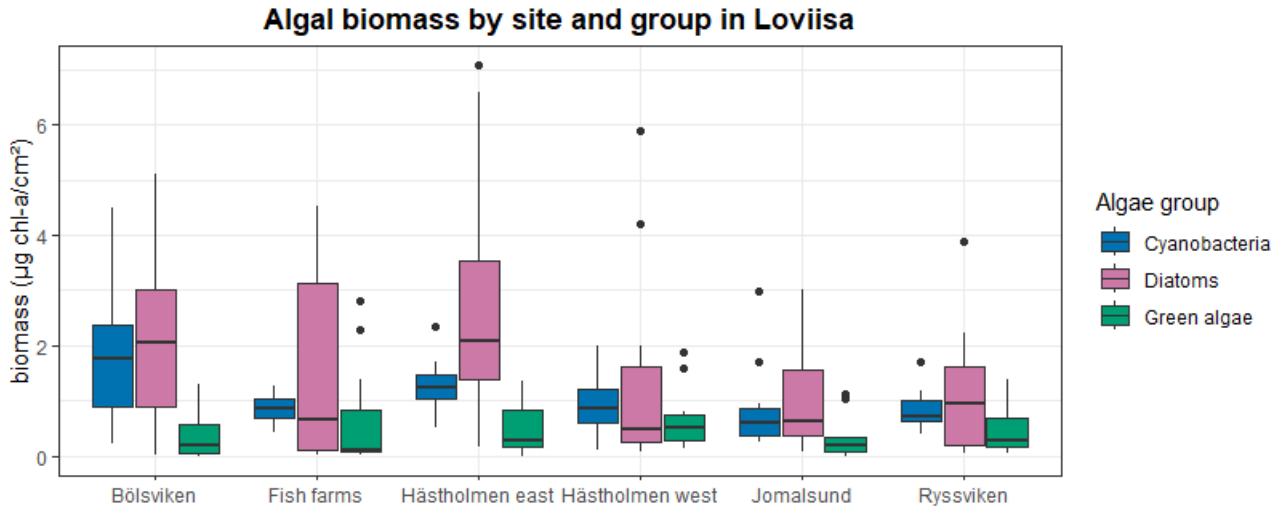

Figure 10. Algal biomass by site and group in Loviisa. Variation at each site represents the temporal variation of biomass values. Hästholmen west is next to the cooling water intake channel, while Hästholmen east is next to the discharge outlet. The box represents the interquartile, while the whiskers show the temporal range of the data. Outliers are shown by the dots, and the lines inside the boxes represent the median values at each site.

Total algal biomass values showed variation between different sites in Loviisa (Figure 11). The highest total biomass was measured at Bölsviken (median 4.8 µg chl-a/cm²) and Hästholmen east (median 4.3 µg chl-a/cm²). These two sites, along with Fish farms, also displayed the greatest range, as the highest total biomass was measured at Hästholmen east (8.4 µg chl-a/cm²). Overall lower median biomass values were measured at Hästholmen west, Jomalsund and Ryssviken, where medians remained under 2.5 µg chl-a/cm². Jomalsund and Ryssviken also showed smaller temporal range of total biomass values than the other sites.

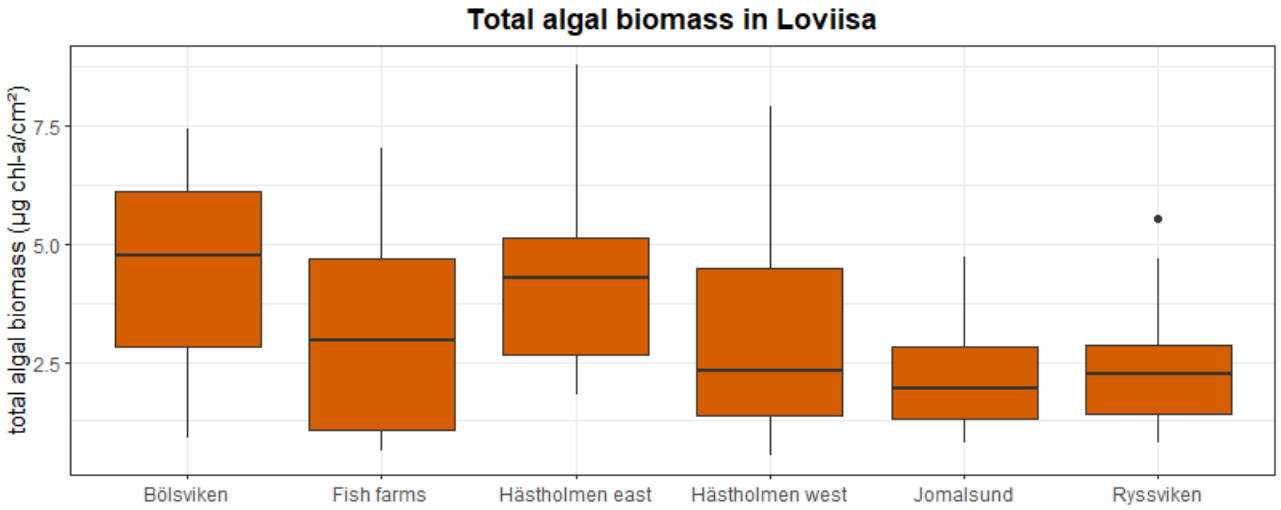

Figure 11. Total algal biomass by site in Loviisa. Variation at each site represents the temporal variation of biomass values. Hästholmen west is next to the cooling water intake channel, while Hästholmen east is next to the discharge outlet. The box represents the interquartile, while the whiskers show the temporal range of the data. Outliers are shown by the dots, and the lines inside the boxes represent the median values at each site.

General linear modeling (GLM) suggested that the most significant factors explaining total algal biomass were water temperature and sampling day (Table 1). Both variables had a positive influence on algal biomass values, though the effect of sampling day was much greater. Water pH levels had a significant negative effect for total algal biomass. The effect of water level approached significance but remained just over $p < 0.05$ threshold, with a similar negative effect to water pH. Other variables had much lower, non-significant effects. The model yielded a high explained deviance of 54.7%, which suggests the variables explained more than half of total algal biomass variation.

Table 1. Results of GLM analysis for the total algal biomass across all sites in Loviisa.

The variables were scaled using base R function scale(), represented by "sc" in the names. Scaling the variables improves the comparability of the variables, however, it also changes the interpreting of the model. Instead of a direct decrease or increase in the unit, the estimate indicates the effect of a one standard deviation increase in that variable. Bolded variables had a statistically significant effect.

Explained deviance = 54.7%. (Significance: . p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001)

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.04778	0.05558	18.850	< 2e-16 ***
water_level_median_sc	-0.10958	0.05698	-1.923	0.058901 .
temperature_sc	0.21243	0.06103	3.481	0.000906 ***
pH_sc	-0.11987	0.05874	-2.041	0.045404 *
TN_sc	-0.11865	0.26372	-0.450	0.654289
TP_sc	0.02679	0.26309	0.102	0.919219
log_conductivity_sc	0.02573	0.06250	0.412	0.681972

sampling_day_sc	0.55731	0.05979	9.320	1.57e-13 ***

R-code: glm(formula = total_mean ~ water_level_median_sc + temperature_sc + pH_sc + TN_sc + TP_sc + log_conductivity_sc + sampling_day_sc, family = Gamma(link = "log"), data = data_loviisa)

The effects of environmental variables differed among algal groups, and therefore group-specific models were analysed separately. For cyanobacteria biomass, only water temperature was found to have a significant effect (Table 2). Water pH levels approached significance with a negative effect, which suggests water chemistry could have a secondary influence after temperature. The positive effect of water temperature indicates that cyanobacteria biomass increased with higher water temperatures, which aligns with the findings in the total algal biomass model. Notably, although often associated with cyanobacterial blooms, total dissolved phosphorus and nitrogen concentrations were not significant in the model. Overall, the model had a low explained deviance, which indicates that other unmeasured variables contribute more to cyanobacteria biomass variation.

Table 2. Results of GLM analysis for cyanobacteria biomass across all sites in Loviisa.

The variables were scaled using base R function scale(), represented by “sc” in the names. Scaling the variables improves the comparability of the variables, however, it also changes the interpreting of the model. Instead of a direct decrease or increase in the unit, the estimate indicates the effect of a one standard deviation increase in that variable. Bolded variables had a statistically significant effect.

Explained deviance = 14.5%. (Significance: . p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001)

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.06803	0.07977	0.853	0.3970
water_level_median_sc	0.04847	0.08177	0.593	0.5554
temperature_sc	0.19474	0.08759	2.223	0.0297 *
pH_sc	-0.15014	0.08430	-1.781	0.0797 .
TN_sc	-0.22537	0.37848	-0.595	0.5536
TP_sc	0.18085	0.37758	0.479	0.6336
log_conductivity_sc	0.05570	0.08970	0.621	0.5369
sampling_day_sc	0.10607	0.08582	1.236	0.2210

R-code: glm(formula = cyano_mean ~ water_level_median_sc + temperature_sc + pH_sc + TN_sc + TP_sc + log_conductivity_sc + sampling_day_sc, family = Gamma(link = "log"), data = data_loviisa

The GLM analysis for green algae indicated that the most significant variable was conductivity, with a very strong positive effect (Table 3). Additionally, sampling day had a significant positive effect, which suggests there was a temporal trend over the course of the summer and autumn. Similarly to the model for cyanobacteria, water pH approached significance, however, the effect was positive for green algae. The model also had a higher

explained deviance than the model for cyanobacteria had, which indicated that the measured variables fit better for explaining green algae biomass variation.

Table 3. Results of GLM analysis for green algae biomass across all sites in Loviisa.

The variables were scaled using base R function scale(), represented by “sc” in the names. Scaling the variables improves the comparability of the variables, however, it also changes the interpreting of the model. Instead of a direct decrease or increase in the unit, the estimate indicates the effect of a one standard deviation increase in that variable. Bolded variables had a statistically significant effect.

Explained deviance = 20.8%. (Significance: . p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001)

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.91676	0.11861	-7.729	9.67e-11 ***
water_level_median_sc	-0.08695	0.12158	-0.715	0.47709
temperature_sc	0.21528	0.13023	1.653	0.10320
pH_sc	0.24261	0.12534	1.936	0.05734 .
TN_sc	0.27178	0.56272	0.483	0.63076
TP_sc	-0.25100	0.56138	-0.447	0.65631
log_conductivity_sc	0.58645	0.13337	4.397	4.23e-05 ***
sampling_day_sc	0.41510	0.12759	3.253	0.00182 **

R-code: glm(formula = green_mean ~ water_level_median_sc + temperature_sc + pH_sc + TN_sc + TP_sc + log_conductivity_sc + sampling_day_sc, family = Gamma(link = "log"), data = data_loviisa)

The GLM for diatom biomass explained the most deviance of all models tested in Loviisa with a high explained deviance of 64.8%, and compared to the other models, the GLM for diatoms resulted in more significant variables (Table 4). The most significant variable was sampling day, which had a very strong positive effect. Water temperature also showed a strong positive effect, while the effect of water level was negative. As with the other groups, water pH only approached significance with a negative effect, and nutrient concentrations did not have a significant influence on biomass.

Table 4. Results of GLM analysis for benthic diatom biomass across all sites in Loviisa.

The variables were scaled using base R function scale(), represented by “sc” in the names. Scaling the variables improves the comparability of the variables, however, it also changes the interpreting of the model. Instead of a direct decrease or increase in the unit, the estimate indicates the effect of a one standard deviation increase in that variable. Bolded variables had a statistically significant effect.

Explained deviance = 64.8%. (Significance: . p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001)

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.01718	0.08898	-0.193	0.8472
water_level_median_sc	-0.48412	0.09121	-5.308	1.48e-06 ***
temperature_sc	0.40092	0.09770	4.104	0.00117 ***
pH_sc	-0.18552	0.09403	-1.973	0.052831 .

TN_sc	-0.28476	0.42217	-0.675	0.502420
TP_sc	0.06408	0.42117	0.152	0.879551
log_conductivity_sc	-0.09547	0.10006	-0.954	0.343603
sampling_day_sc	1.16372	0.09572	12.157	< 2e-16 ***

R-code: glm(formula = diatoms_mean ~ water_level_median_sc + temperature_sc + pH_sc + TN_sc + TP_sc + log_conductivity_sc + sampling_day_sc, family = Gamma(link = "log"), data = data_loviisa)

5.2 Olkiluoto

5.2.1 Environmental variables

Water temperature in Olkiluoto shows a similar temporal trend compared to observations from Loviisa. First and last sampling days showed cooler temperatures, while temperatures peaked midsummer (Figure 12). Olkiluoto west differentiated from the other sites, as it had overall warmer water temperatures during the sampling period, and the highest temperature was measured at +31.8°C. Olkiluoto east had the lowest temperatures in general, though the measurements at all the sites besides Olkiluoto west were within 3°C of each other on every individual sampling day.

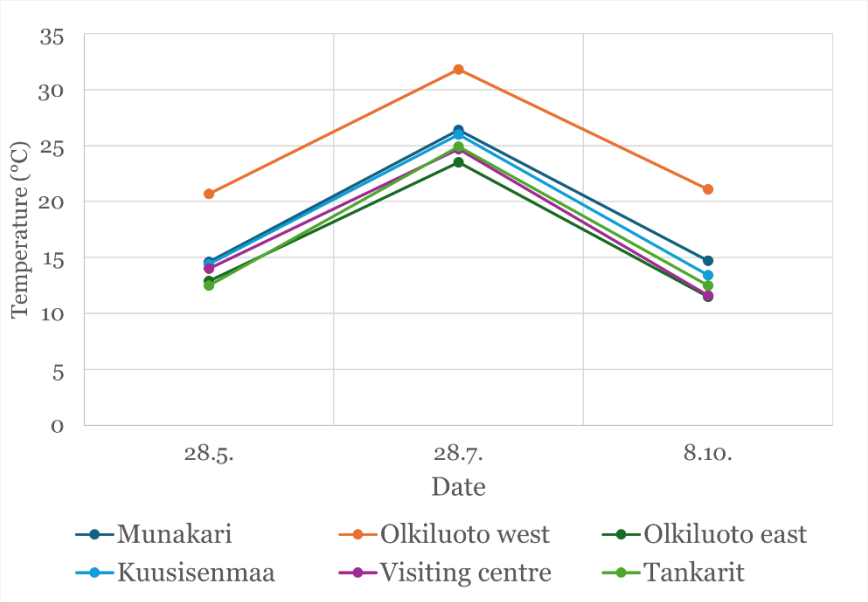

Figure 12. Variation in water temperature at the sampling sites in Olkiluoto during the sampling period in 2025.

Water pH levels ranged from 7.3 to 8.8. Similarly to measurements from Loviisa, water pH had very close median and mean values (8.3 and 8.2), which suggests a symmetric distribution and no strong skew in the data. The middle 50% of the data lied between 8.1

and 8.5. Water pH indicated more differences between the sites than water temperature, as Munakari, Olkiluoto west, Tankarit and Olkiluoto east exhibited an increase between the first and second sampling, while Kuusisenmaa and Visiting centre showed a decrease (Figure 13). However, all six sites had higher pH levels in the first sampling in May, and lower pH levels in the finals sampling in October, suggesting similarities in seasonal differences between the sites.

Water conductivity ranged between 9745-10395 µS/cm. The median value was 9994 µS/cm and the mean 10016 µS/cm. Conductivity varied between sites and showed a temporal trend similar to water pH; all sites had a higher conductivity at the end of the sampling compared to the beginning (Figure 14). The six sites showed somewhat different trends. Munakari and Kuusisenmaa had nearly same values in the first and second sampling and then had a similar increase in the final sampling, while Olkiluoto east, Olkiluoto west, and Tankarit had higher values in both the second and the final sampling. Finally, Visiting centre differentiated from the other sites and was the only site to have a slight decrease between the second and final sampling.

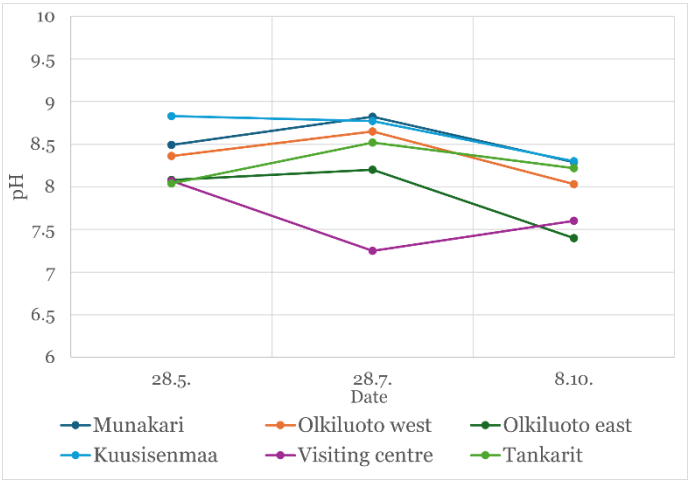

Figure 13. Variation in water pH levels at the sampling sites in Olkiluoto during the sampling period.

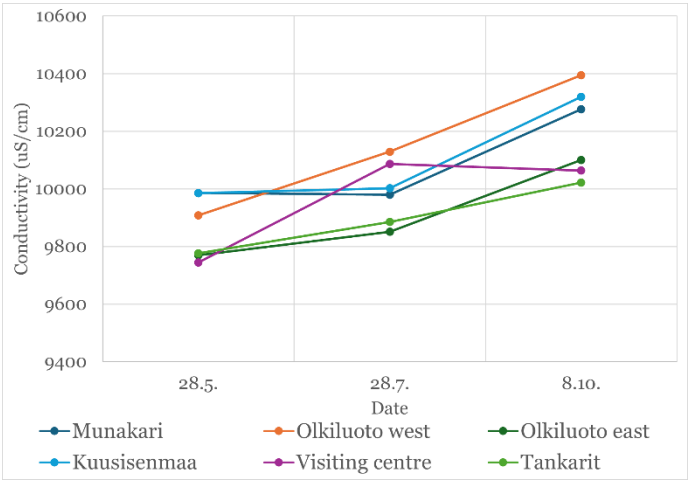

Figure 14. Variation in water conductivity (µS/cm) at the sampling sites in Olkiluoto during the sampling period.

Total nitrogen (TN) had a mean concentration of 0.558 mg/l and a median concentration of 0.538 mg/l. The lower quartile was 0.513 mg/l, and the higher quartile was 0.572 mg/l. These values indicate that there was little variation in TN concentration during the sampling period. Most sites showed a seasonal trend and reached their highest TN concentrations in the second sampling (Figure 15). However, compared to the other sites, Olkiluoto west emerged as an outlier as it had considerably higher TN concentrations on the first sampling and saw a big decrease on the second sampling. Olkiluoto east also

differed from the other sites, as TN values decreased between the first and second sampling, and then increased between the second and the last sampling.

Total phosphorus (TP) had a mean concentration of 31.4 µg/l, and a median concentration of 25.1 µg/l (Figure 16). The lower quartile was 21.2 µg/l, and the higher quartile was 28.3 µg/l. TP concentration showed similar variability between the sites as TN concentration. Most sites had their maximum TP concentration on the first sampling, and the values remained moderately steady. TP concentrations at Olkiluoto west and Olkiluoto east were similar to the TN concentrations there, as the first sampling measured the maximum TP concentration of 146 µg/l in Olkiluoto west, and Olkiluoto east showed a similar temporal trend as it did in the variation of TN concentration.

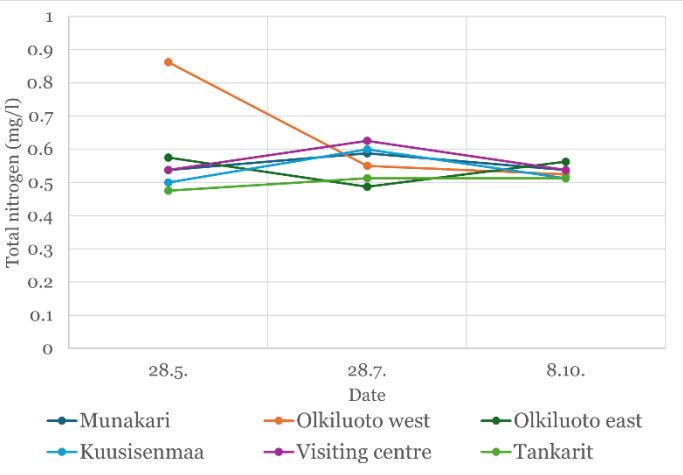

Figure 15. Total nitrogen (mg/l) at each site in Olkiluoto during the sampling period.

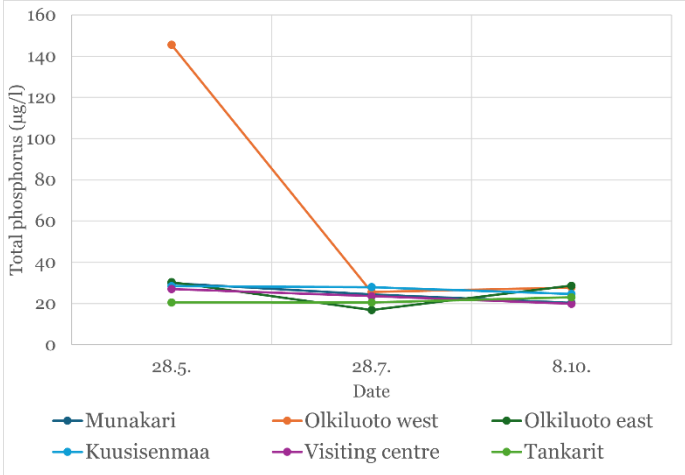

Figure 16. Total phosphorus (µg/l) at each site in Olkiluoto during the sampling period.

5.2.2 Benthic algal biomass

In Olkiluoto, the composition of benthic algal biomass was dominated by cyanobacteria, with moderate diatom and low green algae biomass values (Figure 17). The highest cyanobacteria biomass was measured in Kuusisenmaa, where the values ranged from 0.7 to 6.1 µg chl-a/cm², with a median value of 2.4. Overall, cyanobacteria medians were between 0.3 and 2.4 µg chl-a/cm². Compared to Loviisa where diatoms dominated many of the sites, they did not show as much of variation between sites in Olkiluoto. Diatom values remained moderate compared to the other groups, and median values ranged from 0.1 to 1.8 µg chl-a/cm². Finally, green algae appearance was low at all sites, as median values ranged from 0.1 to just 0.4 µg chl-a/cm². It is worth noting that the biomass composition

at Visiting centre was noticeably different than at the other sites; while cyanobacteria were dominant elsewhere, diatoms were the most abundant group with almost no green algae biomass.

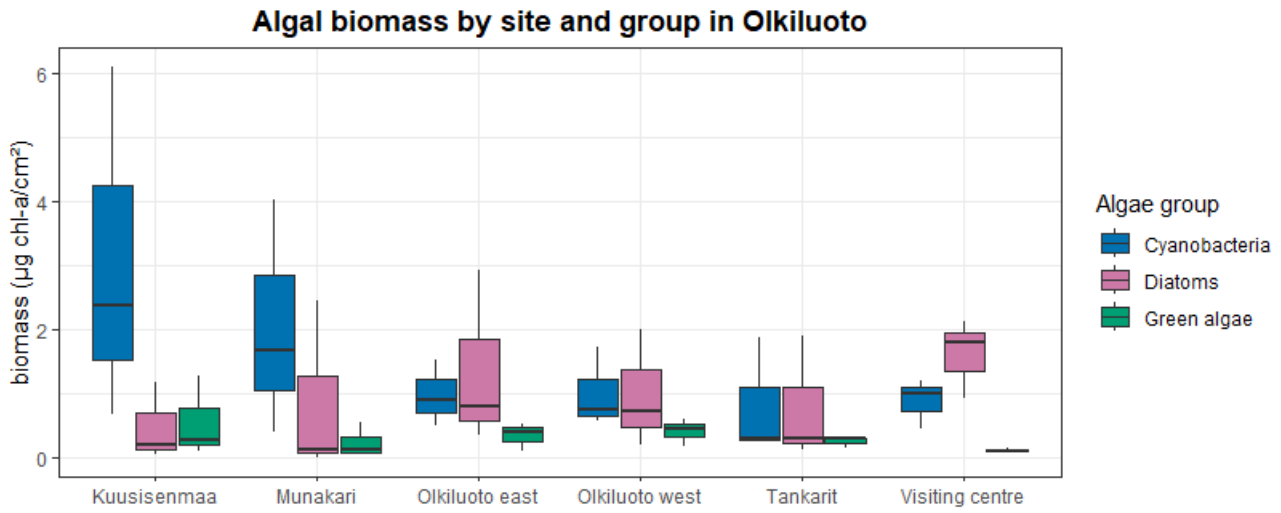

Figure 17. Algal biomass by site and group in Olkiluoto. Variation at each site represents the temporal variation of biomass values. Olkiluoto east is next to the cooling water intake channels, while Olkiluoto west is next to the discharge outlet. The box represents the interquartile, while the whiskers show the temporal range of the data. The lines inside the boxes represent the median values at each site. Unlike in Loviisa, algal biomass values showed no outliers at different sites in Olkiluoto.

The total algal biomass in Olkiluoto indicated the sampling sites represented two different trends. Although all sites showed a strong skew in the biomass totals, Munakari, Olkiluoto east, Olkiluoto west and Tankarit had median values close to the lower quartile, while Kuusisenmaa and Visiting centre had median values close to the higher quartile (Figure 18). Sites also differed in their biomass variability. Greatest variation was measured at Munakari, where both the highest and the lowest total algal biomass values were measured (min = 0.5, max = 7.0). Variability in Olkiluoto west was the opposite as the values ranged only from 2.0 to 3.0 µg chl-a/cm², which suggests little fluctuation in total biomass over the sampling period.

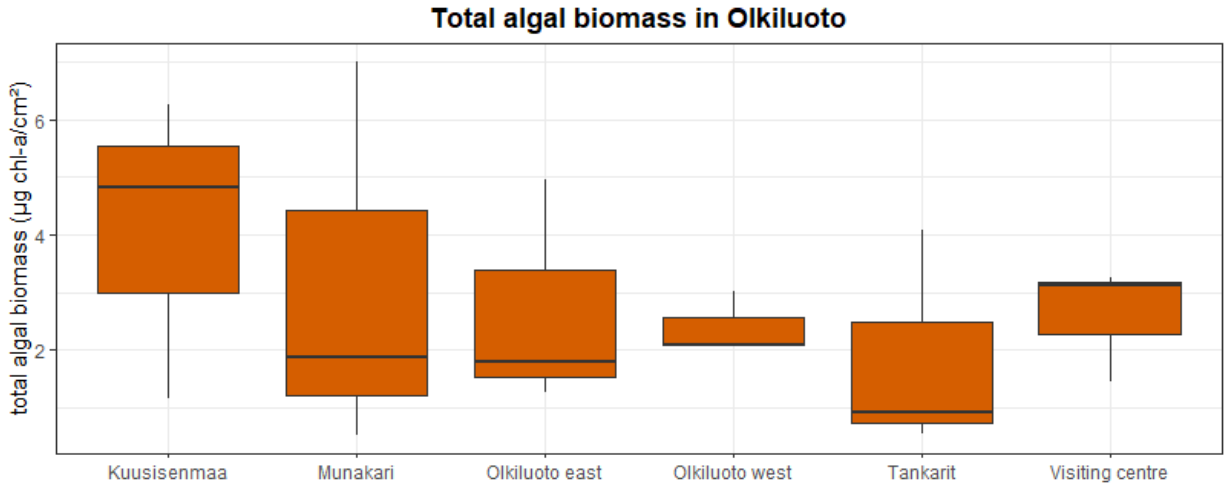

Figure 18. Total algal biomass by site in Olkiluoto. Variation at each site represents the temporal variation of biomass values. Olkiluoto east is next to the cooling water intake channels, while Olkiluoto west is next to the discharge outlet. The box represents the interquartile, while the whiskers show the temporal range of the data. Outliers are shown by the dots, and the lines inside the boxes represent the median values at each site.

General linear modeling (GLM) indicated that only total dissolved nitrogen had significant effect on total algal biomass (Table 5). The effect was very strongly positive, which suggests higher nitrogen concentrations lead to higher total algal biomass. The model also yielded a very high explained deviance of 78.9%.

Table 5. Results of GLM analysis for the total algal biomass across all sites in Olkiluoto.

The variables were scaled using base R function scale(), represented by “sc” in the names. Scaling the variables improves the comparability of the variables, however, it also changes the interpreting of the model. Instead of a direct decrease or increase in the unit, the estimate indicates the effect of a one standard deviation increase in that variable. Bolded variables had a statistically significant effect.

Explained deviance = 78.6%. (Significance: . p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001)

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.82409	0.09773	8.432	7.41e-06 ***
water_level_median_sc	0.69164	2.50262	0.276	0.7879
temperature_sc	-0.24078	0.38526	-0.625	0.5460
pH_sc	0.19340	0.13084	1.478	0.1702
TN_sc	0.84524	0.32813	2.576	0.0276 *
TP_sc	-0.56464	0.36724	-1.538	0.1552
log_conductivity_sc	0.04422	0.23158	0.191	0.8524
sampling_day_sc	-0.07034	2.59364	-0.027	0.9789

R-code: glm(formula = total_mean ~ water_level_median_sc + temperature_sc + pH_sc + TN_sc + TP_sc + log_conductivity_sc + sampling_day_sc, family = Gamma(link = "log"), data = data_olkiluoto)

The effects of environmental variables on each algae group varied also in Olkiluoto. For cyanobacteria, GLM analysis indicated that total dissolved nitrogen as well as water temperature and pH levels were significant (Table 6). Unlike in Loviisa, the effect of water temperature was strongly negative on cyanobacteria in Olkiluoto. Water pH and total dissolved nitrogen concentration had positive effects. Similarly to the total algal biomass model, the GLM for cyanobacteria yielded a very high explained deviance of 81.1%. This suggests that water temperature, pH and nitrogen concentrations were the most important variables for cyanobacteria biomass variation.

Table 6. Results of GLM analysis for cyanobacteria biomass across all sites in Olkiluoto.

The variables were scaled using base R function scale(), represented by "sc" in the names. Scaling the variables improves the comparability of the variables, however, it also changes the interpreting of the model. Instead of a direct decrease or increase in the unit, the estimate indicates the effect of a one standard deviation increase in that variable. Bolded variables had a statistically significant effect.

Explained deviance = 81.1%. (Significance: . p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001)

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.07447	0.10860	0.686	0.50844
water_level_median_sc	5.64411	2.78079	2.030	0.06984 .
temperature_sc	-1.08692	0.42809	-2.539	0.02941 *
pH_sc	0.54629	0.14538	3.758	0.00374 **
TN_sc	1.10169	0.36460	3.022	0.01286 *
TP_sc	-0.48695	0.40806	-1.193	0.26928
log_conductivity_sc	0.25300	0.25732	0.983	0.34871
sampling_day_sc	-5.13665	2.88193	-1.782	0.10502

R-code: glm(formula = cyano_mean ~ water_level_median_sc + temperature_sc + pH_sc + TN_sc + TP_sc + log_conductivity_sc + sampling_day_sc, family = Gamma(link = "log"), data = data_olkiluoto)

For green algae biomass, no significant variables were found in the GLM analysis (Table 7). Water level and sampling day both had a very high estimate value, although both remained non-significant with large standard deviation errors. While still considered a high percentage in an ecological setting, the GLM for green algae also yielded the lowest explained deviance of 45.8% of all three algae groups.

Table 7. Results of GLM analysis for green algal biomass across all sites in Olkiluoto.

The variables were scaled using base R function scale(), represented by “sc” in the names. Scaling the variables improves the comparability of the variables, however, it also changes the interpreting of the model. Instead of a direct decrease or increase in the unit, the estimate indicates the effect of a one standard deviation increase in that variable.

Explained deviance = 45.8%. (Significance: . p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001)

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-1.29536	0.20523	-6.312	8.78e-05 ***
water_level_median_sc	-2.15802	5.25534	-0.411	0.690
temperature_sc	0.17535	0.80903	0.217	0.833
pH_sc	0.04494	0.27476	0.164	0.873
TN_sc	-0.35870	0.68905	-0.521	0.614
TP_sc	0.24965	0.77118	0.324	0.753
log_conductivity_sc	0.30568	0.48631	0.629	0.544
sampling_day_sc	2.29617	5.44647	0.422	0.682

R-code: glm(formula = green_mean ~ water_level_median_sc + temperature_sc + pH_sc + TN_sc + TP_sc + log_conductivity_sc + sampling_day_sc, family = Gamma(link = "log"), data = data_olkiluoto)

Water pH was found to be the only significant variable for diatom biomass in the GLM analysis (Table 8). The effect was strongly negative, indicating that diatom biomass decreased with increasing pH. Like the other models in Olkiluoto, the model had a high explained deviance of 66.3%.

Table 8. Results of GLM analysis for benthic diatom biomass across all sites in Olkiluoto.

The variables were scaled using base R function scale(), represented by “sc” in the names. Scaling the variables improves the comparability of the variables, however, it also changes the interpreting of the model. Instead of a direct decrease or increase in the unit, the estimate indicates the effect of a one standard deviation increase in that variable. Bolded variables had a statistically significant effect.

Explained deviance = 66.3%. (Significance: . p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001)

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.47363	0.16926	-2.798	0.01885 *
water_level_median_sc	-6.13663	4.33411	-1.416	0.18719
temperature_sc	0.99877	0.66721	1.497	0.16529
pH_sc	-0.74412	0.22659	-3.284	0.00823 **
TN_sc	-0.35290	0.56827	-0.621	0.54849
TP_sc	0.01676	0.63600	0.026	0.97950
log_conductivity_sc	-0.27326	0.40106	-0.681	0.51112
sampling_day_sc	6.94480	4.49174	1.546	0.15311

R-code: glm(formula = diatoms_mean ~ water_level_median_sc + temperature_sc + pH_sc + TN_sc + TP_sc + log_conductivity_sc + sampling_day_sc, family = Gamma(link = "log"), data = data_olkiluoto)

6 Discussion

6.1 Effect of water temperature on benthic algal biomass

The findings of this study indicate that water temperature and thermal effluent influence benthic algal biomass. Overall, especially Loviisa had generally higher total algal biomass near the cooling water discharge outlet where temperatures stayed higher than the intake channel side, which had lower water temperatures and lower biomass values throughout the entire sampling. This is indicative that thermal effluent may affect benthic algal biomass, which is also supported by the study on phytoplankton biomass in Loviisa by Ilus and Keskitalo (2008), who found that water temperature was indeed more significant near the discharge outlet. However, in the present study, the responses to higher water temperatures varied between locations and algae groups. In Loviisa, increased water temperature was generally associated with increased algal biomass, whereas in Olkiluoto both positive and negative responses were observed depending on the algae group. Compared to findings in Loviisa, Olkiluoto also showed a weaker contrast in biomass values between the sites near the cooling water intake channels and the discharge outlet, and the effect of warmer water temperatures to total algal biomass was fairly small.

Total opposite effects of water temperature in the two study locations suggest that water temperature can have varying effects depending on the environmental conditions, and the effects cannot be generalized across locations or different algae groups. Thus, the response to water temperature appears to vary depending on the dominant benthic algal groups present in the community. These differences in between locations are consistent with previous research showing that the effects of temperature on benthic algae are not alike across different environments. For example, Patrick et al. (2012) observed increased benthic algal biomass under elevated temperatures in controlled laboratory conditions, whereas Shurin et al. (2024) observed decreases in biomass in high-latitude freshwater ponds with similar temperature variation. These different outcomes support the interpretation that the effects of water temperature are strongly system specific and as the study by Ilus and Keskitalo (2008) highlighted, are likely directed by complex interactions with other environmental variables as well.

The effects of water temperature on different algae groups varied between the two study locations, suggesting that group-specific responses are also dependent on local environmental conditions. In Loviisa, all groups showed generally moderate positive

responses to higher water temperatures, although the effects were statistically significant only for cyanobacteria and diatoms. In contrast, the more variable responses observed in Olkiluoto, including a negative response in cyanobacteria, suggest that other environmental factors may have affected or heavily weakened the effects of water temperature there. These differences may reflect variation in ecological conditions between the study sites and locations, which can influence how different algal groups respond to higher water temperatures or variation in other environmental factors.

The importance of local environmental conditions in shaping temperature responses is supported by previous studies. Mahdy et al. (2015) found a positive and significant correlation between water temperature and benthic algal biomass and suggested that relatively low nutrient availability favoured species adapted to conditions with lower nutrient concentrations, which highlights the effects of water temperature. In this study, phosphorus concentrations were of a similar magnitude to those reported by Mahdy et al. (2015), which is consistent with the finding that water temperature had mostly positive effects while nutrient concentrations had little effect. In contrast, Sapucaia et al. (2024) reported negative effects of increased water temperature on benthic algal biomass under eutrophic conditions, indicating that nutrient-rich environments may alter or even reverse the direction of temperature effects. Together, these findings suggest that the relationship between water temperature and benthic algal biomass is closely linked to nutrient availability, and that the effects of water temperature cannot be interpreted independently of other environmental conditions.

In addition to spatial variation, water temperature also showed a temporal trend from early summer to autumn, suggesting that seasonal changes may have contributed to observed biomass variations as well. Total algal biomass generally increased as the summer progressed, which further supports the importance of seasonal dynamics to benthic algal biomass development during the study period. This indicates that water temperature effects are at least partially tied to other seasonal drivers such as light and nutrient availability, and while light availability was not measured in this study it has been shown to strongly influence benthic algal productivity in previous studies (Mosisch et al., 2001; Schiller et al., 2007). Temperature could also have direct effects on the temporal variation, as for example Ilus and Keskitalo (2008) suggested it may lengthen the growing season, leading to enhanced biomass growth.

6.2 Effects of other environmental factors on benthic algal biomass

In addition to water temperature, other environmental variables such as pH, nitrogen and phosphorus concentrations, conductivity, water level and seasonal variation influenced benthic algal biomass patterns in both study locations (Table 9). The findings of this study suggest that the effects of environmental variables on benthic algae are strongly context-dependent and influenced by local environmental conditions, suggesting that benthic algal biomass is shaped by interactions between multiple environmental factors rather than by single variables acting independently. This also highlights one of the main sources of uncertainty in the study: the sampling sites differed greatly from each other environmentally, which complicates the interpretation and comparison of the results. For example, Jomalsund in Loviisa had considerably lower conductivity values than the other sampling sites, likely due to freshwater influence from Kymijoki river flowing into the coastal area near the site. Similarly, in Olkiluoto, Tankarit was located farther from the other sampling sites and near another major freshwater inflow Eurajoki river, suggesting that it may have represented a somewhat different aquatic environment compared to the other sampling sites.

Table 9. Algae groups and the environmental variables and their effects in Loviisa and Olkiluoto.

If the variable was statistically significant in the GLM analysis, the increasing or decreasing effect is marked with + or -. The significance is marked in brackets after the direction of the effect. Non-significant variables are left blank. L = Loviisa, OL = Olkiluoto. (Significance: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.)

	total algal biomass (L)	total algal biomass (OL)	cyanobacteria (L)	cyanobacteria (OL)	green algae (L)	green algae (OL)	diatoms (L)	diatoms (OL)
water level median				- (*)			- (***)	
temperature	+ (***)		+ (*)	- (**)			+ (***)	
pH	- (*)			+ (**)				- (**)
TN		+ (*)		+ (***)				
TP								
conductivity					+ (***)		+ (***)	
sampling day	+ (***)				+ (**)		+ (**)	

Nutrient availability appeared to have a relatively limited influence on benthic algal biomass in this study, as statistically significant effects were observed only for total nitrogen in Olkiluoto. This contrasts with many previous studies where nitrogen and

phosphorus concentrations have been identified as major or limiting factors for benthic algal growth (Bécares et al., 2008; Hillebrand & Kahlert, 2001; Schiller et al., 2007), and in the same study location for phytoplankton (Ilus & Keskitalo, 2008). One possible explanation for the difference to previous studies is that nutrient concentrations may have remained within ranges that did not strongly limit benthic algal growth during the sampling period. Alternatively, the effects of nutrients may have been outweighed by other environmental factors, such as temperature or seasonal variation, which would align with the findings on the effects of water temperature and the study by Mahdy et al. (2015). Regardless of the explanation for the weak effect from nutrient concentrations, the findings would indicate that they were not a limiting resource for benthic algal biomass growth in this study.

Chemical conditions appeared to affect benthic algae groups differently between the two study locations, and the observed effects were not fully consistent across algae groups either. In Loviisa, conductivity measurements were higher with increased green algae biomass, while pH showed a weak negative relationship with total algal biomass, indicating the species preferred more acidic water. In contrast, pH in Olkiluoto had a positive effect on cyanobacteria biomass but affected diatom biomass negatively. These different responses suggest that algae groups in these two locations may vary in their tolerance or sensitivity to chemical conditions, and that local environmental conditions influence how strongly these variables shape benthic algae community composition. Although pH may not appear to have a strong effect on overall benthic algal biomass, it may still play an important role in shaping species richness (Eloranta et al., 2007). However, the interpretation of pH-related results should be approached cautiously due to limitations in the dataset. During sampling in Loviisa on the 21st of August, the pH measuring device failed, and the missing values were imputed using measurements from the following sampling day to maintain continuity in the modeling process. As a result, the pH data may not fully represent the natural short-term variation between the August and September sampling periods.

Seasonal variation and hydrological conditions appeared to influence benthic algal development, particularly in Loviisa. This is supported by the observed effects of sampling day and water level on diatoms and total algal biomass. The positive relationship between sampling day and some algae groups suggests that seasonal progression from early summer towards autumn affected biomass growth during the sampling period. Seasonal

changes in factors such as light availability, temperature and overall succession likely contributed to these findings. In addition, the negative effect of water level on diatom biomass in Loviisa, and on cyanobacteria biomass in Olkiluoto, may indicate that variation in water level is connected to benthic algae attachment to growing substrate.

6.3 Uncertainty and study limitations

In addition to differences in sampling site environments and broken pH measurement device, the study also had other limitations and causes of uncertainty related to sampling, environmental variability and statistical modelling. These limitations should be considered when interpreting the reliability of the findings.

The sampling during the field work introduced several possible obstacles that may have influenced the data and results. Due to fairly large variation in water levels during the sampling, the sampled rocks may not have been submerged for sufficient time, as the availability and consistency of suitable sampling surfaces varied. In addition, excessive macroalgae growth on some substrates may have reduced the suitability of the sampled surfaces for benthic algae measurements, potentially introducing errors into biomass estimates in BenthoTorch. The overall sample size was also limited in Olkiluoto, where only three sampling points were available per site. This sparse sampling likely contributed to uncertainty in the findings and reduced the reliability of the statistical comparisons. The limited number of observations in Olkiluoto was also reflected in the descriptive analyses, where boxplots were often strongly skewed. With such a small sample size, individual observations can disproportionately influence median values and interquartile ranges, making visual interpretation less stable and potentially less representative of true variability.

Another key source of uncertainty in this study relates to the differences between sampling sites. The sites were not strictly comparable by their environmental conditions and could not be divided into treatment and control sites due to their differences. As a result, it was difficult to isolate the specific effects of thermal effluent from broader environmental variation or interaction between variables across sampling sites, and as a result, site-specific conditions such as hydrology, geographical setting and proximity to freshwater inflows likely influenced the observed findings. In addition, some important ecological variables were not measured. For example, light availability and grazing pressure, both of

which are known to strongly affect benthic algal communities, were not included in the analysis.

Differences in sampling intensity between locations also affected model performance. Some models, particularly in Olkiluoto, explained an extremely high proportion of deviance, and while this may indicate strong relationships between environmental variables and algal biomass, such high explained deviance values should be interpreted cautiously in ecological studies. Overall, skewed data distributions, sparse sampling, and differences in collinearity between datasets introduce uncertainty into the model results and limit how broadly the findings can be applied, especially for Olkiluoto.

7 Conclusion

This study examined the effects of water temperature and other environmental drivers on benthic algal biomass in coastal areas near nuclear power plants in Loviisa and Olkiluoto. The results showed that water temperature had a mostly positive effect on benthic algal biomass, and biomass levels were generally higher near the cooling water discharge outlets than the intake channels at both study locations, but especially in Loviisa. This suggests that thermal effluent may enhance benthic algal biomass growth in these conditions. However, the results for water temperature were not consistent across all algae groups. In Olkiluoto, the effect of water temperature was negative for cyanobacteria, which contracts the opposite effect for cyanobacteria in Loviisa. Previous literature on the effects of water temperature on benthic algae does support these contrasting findings, as water temperature has been shown to have complicated interactions with other environmental variables. Although in this study setting, the results for Olkiluoto should be interpreted carefully, as the dataset was so small, there was multicollinearity between predictor variables and the GLM analysis yielded very high explained deviance percentages for an ecological study setting. To avoid these uncertainties, the findings of this study demonstrate that this kind of study setting would require a more intensive sampling, rather than the sparse sampling style carried out in Olkiluoto.

In addition to temperature, other environmental variables such as total nitrogen and phosphorus concentrations, conductivity, water pH-levels, water level and sampling day influenced benthic algal biomass. While some significant effects were found, no single environmental factor consistently explained biomass variation across both locations. This indicates that biomass variation cannot be explained by a single environmental variable but rather requires a more complete understanding of the local conditions.

Overall, the findings indicate that benthic algal biomass responses to thermal effluent and environmental drivers are highly context-dependent and cannot be generalized across locations or algal groups. Different algal groups showed varying responses to environmental variables, suggesting that community composition plays an important role in shaping how benthic algae respond to environmental change locally. Biomass variation therefore appears to be controlled by a combination of local environmental conditions rather than a single dominant factor. Despite limitations related to sampling design and environmental variability of the study locations, this study provides insight into benthic

algal responses to thermal effluent near nuclear power plants and highlights the importance of considering local conditions when interpreting ecological responses. These findings also suggest that future research should further examine the interaction between temperature, nutrients and site-specific environmental conditions to better understand the mechanisms affecting variation in benthic algal biomass.

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Appendices

Appendix 1. Photos of the sites during the field work in 2025

Loviisa

Hästholmen east


27.5.


10.6.


23.6.


4.7.


16.7.


29.7.


8.8.


21.8.


1.9.


11.9.


26.9.


10.10.

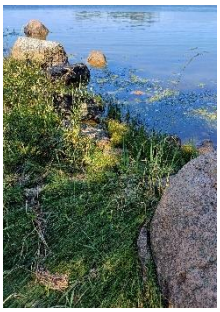
Hästholmen west


27.5.

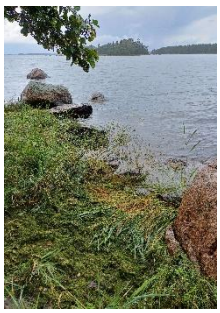

10.6.


23.6.


4.7.


16.7.


29.7.


8.8.


21.8.


1.9.


11.9.


26.9.


10.10.

Fish farms

27.5. 10.6. 23.6. 4.7. 16.7. 29.7.

8.8. 21.8. 1.9. 11.9. 26.9. 10.10.

Jomalsund

27.5. 10.6. 23.6. 4.7. 16.7. 29.7.

8.8. 21.8. 1.9. 11.9. 26.9. 10.10.

Bölsviken


27.5.


10.6.


23.6.


4.7.


16.7.


29.7.


8.8.


21.8.

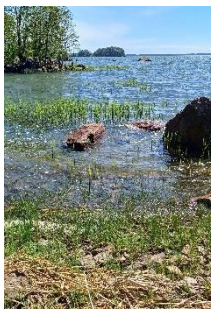

1.9.


11.9.


26.9.


10.10.

Ryssviken


27.5.


10.6.


23.6.


4.7.


16.7.


29.7.


8.8.


21.8.


1.9.


11.9.


26.9.


10.10.

Olkiluoto

Olkiluoto west

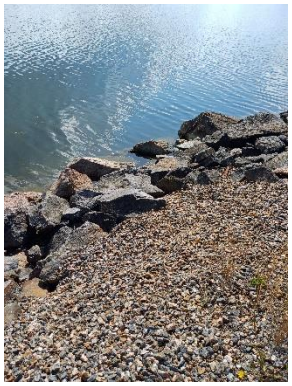
28.5.

28.7.

8.10.

Olkiluoto east

28.5.



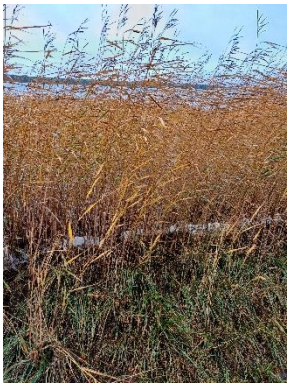
28.7.

8.10.

Visiting centre

28.5.

28.7.



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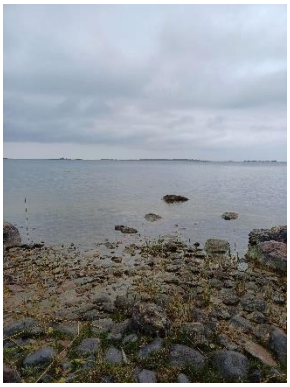
Kuusisenmaa

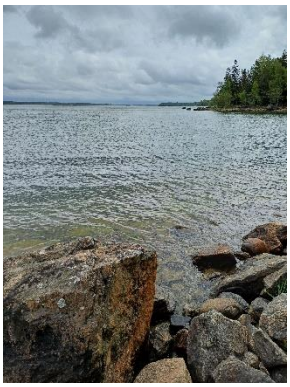


28.5.

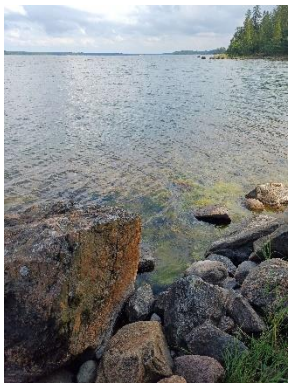
28.7.

8.10.

Tankarit



28.5.



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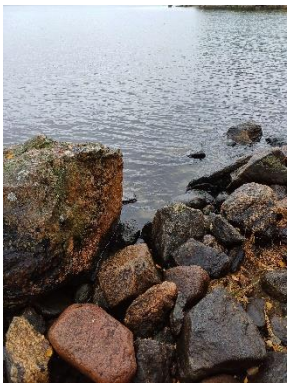
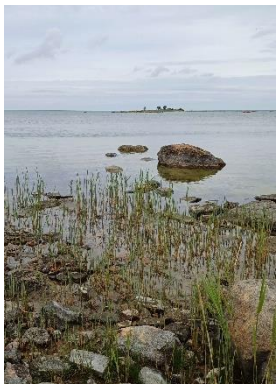


8.10.

Munakari



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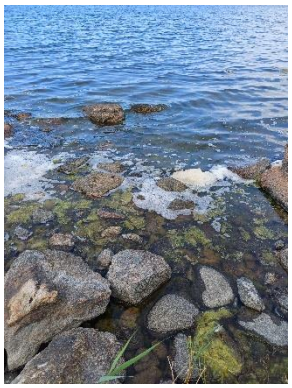

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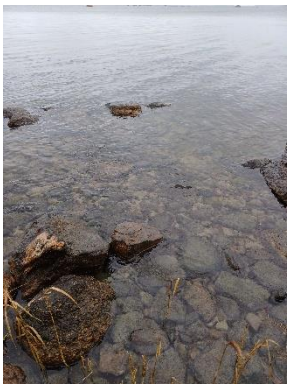

8.10.

Appendix 2. Multicollinearity analysis

Spearman's collinearity analysis for Loviisa dataset

Bolded values indicate multicollinearity between the variables (ρ > 0.70). wl = water level

	TP	TN	temperature	pH	conductivity	wl median	sampling day
TP		0.64	0.13	-0.08	-0.22	-0.001	0.07
TN	0.64		0.25	0.19	-0.4	0.11	0.3
temperature	0.13	0.25		-0.07	-0.22	0.22	-0.19
pH	-0.08	0.19	-0.07		-0.04	-0.05	0.19
conductivity	-0.22	-0.4	-0.22	-0.04		-0.08	-0.29
wl median	-0.001	0.11	0.22	-0.05	-0.08		0.09
sampling day	0.07	0.3	-0.19	0.19	-0.29	0.09	

Spearman's collinearity analysis for Olkiluoto dataset

Bolded values indicate multicollinearity between the variables (ρ > 0.70). wl = water level

	TP	TN	temperature	pH	conductivity	wl median	sampling day
TP		0.48	-0.06	0.19	-0.07	-0.45	-0.45
TN	0.48		0.31	0.001	0.1	-0.08	-0.08
temperature	-0.06	0.31		0.54	0.05	-0.12	-0.12
pH	0.19	0.001	0.54		-0.11	-0.29	-0.29
conductivity	-0.07	0.1	0.05	-0.12		**0.77**	**0.77**
wl median	-0.45	-0.08	-0.12	-0.29	**0.77**		**1**
sampling day	-0.45	-0.08	-0.12	-0.29	**0.77**	**1**	