Long-term spatiotemporal water quality and phytoplankton dynamics in Severn Sound, Ontario: a delisted Great Lakes Area of Concern

by

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An oral defense of this thesis took place on December 8, 2025 in front of the following examining committee:

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Research Supervisor	Dr. Andrea Kirkwood
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The above committee determined that the thesis is acceptable in form and content and that a satisfactory knowledge of the field covered by the thesis was demonstrated by the candidate during an oral examination. A signed copy of the Certificate of Approval is available from the School of Graduate and Postdoctoral Studies.

ABSTRACT

Severn Sound is an embayment system located in south-eastern Lake Huron that was previously designated an Area of Concern (AOC) in 1987 as part of the Great Lakes Water Quality Agreement. The AOC designation was largely due to eutrophication, which has been a historical issue in Severn Sound extensively documented by a water quality and phytoplankton monitoring program since 1973. My thesis research analyzed this long-term dataset representing four embayments within Severn Sound as well as nearshore-offshore water quality in the embayments. I found statistically significant differences across stations in water quality parameters such as total phosphorus, total nitrogen, Secchi disk visibility, and water temperature. Overall decreases in total phosphorus and chlorophyll *a* and increases in Secchi disk visibility illustrate the influences of nutrient reduction strategies, and potential influences from invasive dreissenid mussels. Although an important driver of water quality changes, water temperature change was variable during the study, likely due to site-specific differences and inherent data variability. Generalized Additive Mixed Models showed decreases in total phytoplankton biovolume and different significant drivers across seven major phytoplankton divisions. Permutational Multivariate Analysis of Variance (PERMANOVA) revealed that station, along with period (before, during, and after delisting), and interaction of station and period were significant drivers of phytoplankton community composition. Using redundancy analysis, I found cyanobacterial community assemblages were significantly different both before, during, and after AOC listing, and before and after the zebra mussel invasion, as well as across stations, with period being the highest explanatory variable of community shifts. Generalized Additive Models

revealed a significant difference in environmental drivers of three major cyanobacterial genera, *Aphanizomenon*, *Dolichospermum*, and *Microcystis*. Overall findings indicate that cyanobacterial communities shifted in response to nutrient mitigation, climate, and the zebra mussel invasion. In addition, I found statistically significant differences in nearshore-offshore chlorophyll a, conductivity, total ammonia/ammonium nitrogen, total organic nitrogen, and total phosphorus. A PERMANOVA also revealed that nearshore-offshore water quality was significantly different across region but found no statistical difference in embayments. Overall, these findings can be used to inform management decisions in the Severn Sound region, other Areas of Concern, and regions experiencing eutrophication.

Keywords: Severn Sound; water quality; phytoplankton; cyanobacteria; nearshore-offshore

AUTHOR'S DECLARATION

I hereby declare that this thesis consists of original work of which I have authored. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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STATEMENT OF CONTRIBUTIONS

The work described in Chapter 2 was published in the Journal of Great Lakes Research as: Tyner, A., Chiandet, A., & Kirkwood, A. (2025). Nearly 50 years of water quality monitoring shows improvements and remaining challenges for a delisted Great Lakes Area of Concern. *Journal of Great Lakes Research.* https://doi.org/10.1016/j.jglr.2025.102704. I was responsible for data curation, data analysis, and writing of the manuscript. Content was modified to fit thesis formatting

Chapters 2, 3, and 4 include data provided by the Severn Sound Environmental Association. I performed data curation, data analysis, and writing of this manuscript.

Chapter 4 includes data in which I was responsible for collecting field samples, conducting laboratory analyses, curating, and analyzing data, and writing the manuscript.

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LIST OF ABBREVIATIONS AND SYMBOLS

%	Percent
µg	Micrograms
µS	Micro Siemens
AIC	Akaike Information Criterion
ANOVA	Analysis of variance
AOC	Area of Concern
ARMA	Autoregressive moving average
BUI	Beneficial Use Impairment
Chla	Chlorophyll a
Cond	Conductivity
DO	Dissolved oxygen
DOY	Day of year

GAM	Generalized Additive Model
GAMM	Generalized Additive Mixed Model
GLWQA	Great Lakes Water Quality Agreement
HAB	Harmful algal bloom
L	Liter
LLM	Linear mixed-effect model
LM	Linear model
m	Meter
N:P	Nitrogen:phosphorus
PCA	Principal Component Analysis
PERMANOVA	Permutational analysis of variance
PWQO	Provincial water quality objectives
R^2	Coefficient of determination
RAP	Remedial Action Plan
RDA	Redundancy Analysis
SSEA	Severn Sound Environmental Association
TAN	Total ammonia/ammonium nitrogen
TN	Total nitrogen
TNN	Total nitrate/nitrite nitrogen
TON	Total organic nitrogen
TP	Total phosphorus
TSW	Trent-Severn Waterway
WT	Water temperature
Z_{sd}	Secchi disk depth

Chapter 1. Introduction

1.1 Severn Sound

Severn Sound is located within south-eastern Georgian Bay, Lake Huron on the Canadian side of the Great Lakes (Figure 1.1). As a unique 130-km^2 embayment-system, Severn Sound contains several smaller bays including Penetang Harbour, Outer Harbour, Midland Bay, Hogg Bay, Sturgeon Bay, and Matchedash Bay (Severn Sound Remedial Action Plan, 1988). The Severn Sound watershed is approximately 1000-km^2 and receives drainage from 7 rivers and creeks (Severn Sound Remedial Action Plan, 1993).

Severn Sound is at the western terminus of the Trent-Severn Waterway (TSW), which is a 386-km canal system that connects Lake Huron to Lake Ontario at Trenton, Ontario. Although originally created for transportation of lumber and other supplies, the TSW is now a major source of tourism and recreation, hydro-electrical power, and flood control (Legget, 2015). The Lake Huron watershed varies significantly from the north to south in geology, land use, and ecological features which directly influences water quality. North and eastern regions are covered by Precambrian igneous and metamorphic rocks and are heavily forested and supports many wetlands (Bockheim, 2021). In contrast, the southern shores are covered by sandstone and shale making it more suitable for agriculture (Bockheim, 2021). Georgian Bay is covered by the Precambrian shield with very shallow soils (Severn Sound Remedial Action Plan, 1988).

Figure 1.1. Map of the Severn Sound region including location within the Great Lakes. Watershed boundaries are outlined in black (Ontario Ministry of Natural Resources and Forestry, 2025). PH = Penetang Harbour, OH = Outer Harbour, MB = Midland Bay, TB = Tiffin Basin, HB = Hogg Bay, SB = Sturgeon Bay, MB = Matchedash Bay

The Severn Sound region is used for many purposes including urban, agricultural, natural, and recreational. The urban area of Severn Sound serves both a permanent population as well as a seasonal population during the summer. In 1986, Severn Sound had a permanent population of about 38,000 and a seasonal population of about 40,000 and by 2009 this region had permanent population of about 110,000 and a seasonal population of about 200,000 (Keir Consultants, 1991; Severn Sound Environmental Association, 2009). Severn Sound also supports an agricultural usage of crop production, pasture, and livestock (Severn Sound Remedial Action Plan, 1988). Farming is not well supported in regions of the Georgian bay Fringe and the Simcoe Uplands due to the soil and steep terrain which leaves the region to support more naturalized landscapes including forests and wetlands such as swamps, marshes, and bogs on the eastern side (Severn Sound Remedial Action Plan, 1988). The waters of Severn Sound are used for many activities such as recreational and sports fishing, commercial fishing, boating, swimming, fish and wildlife habitat, hydro-electrical power, flood control, and water supply (Severn Sound Remedial Action Plan, 1988).

The embayments of Severn Sound have been noted to experience differences in water quality since the first observations in 1969 (Veal & Michalski, 1971). These differences have been tied to differences in lake morphometry, geology, and land use. Severn Sound is partially isolated from Georgian Bay by an island archipelago restricting mixing of some areas. In addition, the embayments of Severn Sound are relatively shallow (2-20 m) with water depth being generally deeper on the western side and decreasing towards the eastern side. In the 1970s, Penetang Harbour was noted as having higher concentrations of total phosphorus, chlorophyll *a*, and algal blooms likely due to

morphometry of the harbour preventing mixing (Severn Sound Remedial Action Plan, 1988). Sturgeon Bay on the eastern side of Severn Sound has been noted with having warmer waters due to shallowness supporting warmer temperatures and aquatic plant growth, and limited mixing with the cold waters of Georgian Bay (Severn Sound Remedial Action Plan, 1988). The shallowness of the embayment, limited mixing, as well as agricultural and urban runoff has made this region susceptible to eutrophication and habitat degradation. Since the mid-1960's there has been public concern regarding water quality, specifically excessive algal growth in Severn Sound (Severn Sound Remedial Action Plan, 1988).

1.2 Policy and management

The Great Lakes Water Quality Agreement (GLWQA) was first signed in 1972 by Canada and the United States to restore water quality in the Great Lakes. Multiple amendments have been made since it was originally signed, building on the original goal. In 1987 the GLWQA was amended with the focus of significantly degraded areas within the Great Lakes known as Areas of Concern (AOC). Forty-three AOC were identified which included a list of 14 potential Beneficial Use Impairments (BUI): restrictions on fish and wildlife consumption, tainting of fish and wildlife flavor, degradation of fish wildlife populations, fish tumors or other deformities, bird or animal deformities or reproduction problems, degradation of benthos, restrictions on dredging activities, eutrophication or undesirable algae, restrictions on drinking water consumptions, or taste and odor problems, beach closings, degradation of aesthetics, added costs to agriculture

or industry, degradation of phytoplankton and zooplankton populations, and loss of fish and wildlife habitat (International Joint Commission, 1994).

In addition to AOCs, the 1987 amendment added Remedial Action Plans (RAP), which were actions required for AOC mitigation (International Joint Commission, 1994). These RAPs are a structured and ecologically comprehensive approach to improve BUIs by requiring documentation of the assessment, environmental conditions and impairments (including BUIs), and milestones in restoration. They also include known and potential causes of impairments. After defining and identifying causes of BUIs of the area, RAPs would then evaluate current, planned, and potential remedial measures. Finally, an evaluation of effectiveness of remedial measures is conducted, along with a monitoring process to track remedial measures and environmental changes. The overall goal is that RAPs would allow for the restoration of AOC through thorough assessment and planning (International Joint Commission, 1994).

Excessive algal growth had been a concern in Severn Sound since the mid 1960s (Severn Sound Remedial Action Plan, 1988). This algal growth and degraded water quality had negative impacts on recreational usage as well as influenced shifts in fish community composition, such as a decline in the walleye population (Severn Sound Remedial Action Plan, 1988). Severn Sound was designated as an AOC in the 1987 GLWQA due to multiple BUIs including: restrictions on fish and wildlife consumption, degradation of fish wildlife populations, loss of fish and wildlife habitat, degradation of benthos, degradation of phytoplankton and zooplankton populations, eutrophication or undesirable algae, beach closings, and degradation of aesthetics (Sherman, 2002). With this designation a three-stage RAP was put in place: Stage 1 – description of

environmental conditions and BUIs, Stage 2 – outline objectives, water use goals, and remedial action needed for restoration, Stage 3 – confirmation of restoration (Sherman et al., 2018).

Two major goals of the RAP in Severn Sound was to improve water quality and maintain a healthy ecosystem (Severn Sound Remedial Action Plan, 1993). In addition to these goals, there were also water use goals to ensure that water is swimmable, fish were edible, and fish and aquatic habitats were protected to maintain fish communities (Severn Sound Remedial Action Plan, 1993). Phosphorus sourced from agriculture, urban run-off, and sewage treatment facilities was identified as a key nutrient causing eutrophication in Severn Sound (Severn Sound Remedial Action Plan, 1993). A major focus of restoration in this region was to reduce phosphorus inputs to reduce algae. Delisting objectives in Severn Sound Remedial Action Plan Stage 3 (Sherman, 2002) related to eutrophication were:

- Total phosphorus concentration < 20 µg/L in open waters and < 15 µg/L in Penetang Harbour
- Chlorophyll *a* concentration < 5µg/L in open waters and < 7 µg/L in Penetang Harbour
- Water clarity (Secchi depth) > 3 m / on the bottom in open waters and >2m in Penetang Harbour
- Rooted aquatic plant coverage should be maintained, and distribution should be increased by 30% in Penetang Harbour
- Minimum bottom water dissolved oxygen concentration >5 mg/L

Many remedial actions were taken to reduce eutrophication, improve aquatic habitats, and improve water quality for swimming. This included: (1) improving sewage

plant efficiency and providing additional treatment plants, (2) upgrading private sewage systems, (3) reducing storm water supply, (4) reducing agriculture sources of pollution, (5) reducing sources of erosion, (6) reducing sources of pollution from marine activities, (7) improving and protecting fish and wildlife conditions, (8) preventing contamination, and (9) receiving input and reviewing plans related to remedial actions. The successful implementation of the RAPs and the restoration of BUIs resulted in Severn Sound being delisted as an AOC in 2003 (Sherman, 2002). Currently Severn Sound is one of 10 (three Canadian and seven U.S) out of 43 AOCs to be delisted.

1.3 Water quality and Eutrophication

Water quality reflects the overall environmental condition of aquatic ecosystems, including a range of physical, chemical, and biological parameters, which collectively influences ecological function, biodiversity, and human use. Historically, Severn Sound has experienced significant eutrophication due to excessive nutrient inputs from point sources (i.e., sewage treatment plants) and non-point sources (i.e., agricultural and urban run-off), leading to its designation as an AOC (Severn Sound Remedial Action Plan, 1988; Severn Sound Remedial Action Plan, 1993). Although targeted management efforts through the RAP have led to improvements in water quality, concerns still exist in relation to nutrient levels and frequency and severity of algal blooms.

My thesis research focuses on multiple water quality parameters in Severn Sound. Total phosphorus (TP) represents both dissolved and particulate phosphorus in the water column. Although the anion phosphate (PO_4^{-3}) is the key limiting nutrient driving algal growth and bloom formation (Schindler & Fee, 1974), TP is measured to capture the

entire phosphorus-pool, including other forms of bioavailable phosphorus. Nitrogen is another macronutrient required for growth by algae, but it is typically available at higher concentrations than TP, and therefore not considered to be a consistent growth-limiting nutrient, though co-limitation can be common (Sterner, 2008). To investigate impacts of nitrogen, multiple nitrogen forms were analyzed including total nitrogen (TN), total organic nitrogen (TON), nitrate-nitrite (TNN), and ammonia-ammonium (TAN). These forms distinguish between organic and inorganic sources of nitrogen, which differ in their bioavailability and uptake rates, which can influence phytoplankton abundance and composition by favouring certain taxa over others depending on their nutrient preferences or physiological capabilities (Donald et al., 2011). Chlorophyll *a* (chla) is a universal pigment in all photosynthesizing algal taxa, as well as cyanobacteria, so effectively serves as a proxy for phytoplankton biomass since it is a direct biological response to nutrient availability (Prairie et al., 1989). Water clarity as measured by Secchi disk visibility (Z_{sd}), is influenced by both phytoplankton abundance and is an indicator of lake trophic state (Binding et al., 2024). Together these parameters offer a comprehensive analysis of nutrient enrichment and algal dynamics in Severn Sound.

Eutrophication is a major driver of water quality degradation in freshwater systems, primarily caused by excessive nutrient loading, particularly from phosphorus and nitrogen. Phosphorus is commonly the limiting nutrient in freshwater environments because it has limited natural sources and is less labile than nitrogen (Schindler et al. 2006). However, anthropogenic inputs from agricultural and urban runoff and wastewater treatment plants have led to increased primary production and nuisance and harmful algal blooms (HABs) (Elser et al., 1990; Lewis Jr. & Wurtsbaugh, 2008; Schindler & Fee,

1974). Nitrogen also plays a role in shaping phytoplankton abundance and community composition, particularly in environments where nitrogen-fixing cyanobacteria can become dominant under low N:P (nitrogen:phosphorus) conditions (Paerl, & Otten, 2013). These nutrient-driven process contribute to reduced water clarity, oxygen depletion, and shifts in food web dynamics (Paerl, & Otten, 2013; Smith et al., 1999).

Freshwater ecosystems are increasingly being threatened by anthropogenic impacts such as nutrient loading, land use change, urbanization, and climate variability (Carpenter et al., 1998; O'Neil et al., 2012; Paerl & Paul, 2012). Among the most widespread stressors is nutrient enrichment, which fuels eutrophication and alters ecosystem structure and function (Carpenter et al., 1998; Smith et al, 1999). In addition to nutrient loading, climate change is becoming an increasing concern as it can alter precipitation patterns, increase water temperatures, and extend the growing season for phytoplankton, including HABs (Paerl & Paul, 2012). Together these pressures can be synergistic, creating long-term challenges for water quality management.

Expansion of agriculture, urban areas, and industrial activities in the mid 1900's has contributed to increased nutrient loading and eutrophication in the Great Lakes (Slowinski et al., 2023). This was followed by the GLWQA that worked to reduce impacts to water quality. However, many areas continue to experience degraded water quality, algal blooms, and hypoxia, especially in shallow and enclosed systems such as Severn Sound. In recent years Lake Huron has experienced more oligotrophic conditions, related to efforts to decrease nutrient inputs coupled with the introduction of invasive zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels, which have been shown to impact nutrient cycling by sequestering nutrients for growth,

as well as depositing and returning nutrients to the water column through feces and pseudofeces (Arrnott & Vanni, 1996; Budd et al., 2001; Fisherman et al., 2010; Johengen et al., 1995). Zebra mussels have been shown to decrease phosphorus inputs as well as increase water clarity across the Great Lakes, including Lake Huron (Cha et al., 2011; Dobiesz & Lester, 2009; Fisherman et al., 2010).

In regions such as Severn Sound, nutrient enrichment has caused eutrophication to be a primary concern. While management efforts such as GLWQA and RAP has significantly reduced TP and improved some water quality indicators, spatial and temporal variability in nutrient concentrations and phytoplankton abundance still exists in this region and could be a potential concern for exacerbated algal blooms and a resurgence of eutrophic conditions. While nutrient loading and land use have historically driven water quality changes in Severn Sound, climate change is emerging as an increasingly important influence which can directly and indirectly impact water quality.

1.4 Climate

Anthropogenic climate change is increasingly affecting freshwater ecosystems through a range of mechanisms, including rising temperatures, altered precipitation regimes, and reduced ice cover duration (Döll & Zhang, 2010; Woolway et al., 2022). These mechanisms are all impacting the physical and chemical conditions in the Great Lakes basin. Although various climatic factors influence ecosystem dynamics, this research focuses specifically on changes in water temperature as a potential driver of both water quality and phytoplankton response in the region. In recent years there has been growing scientific attention to water temperature as a key indicator of climate-driven

change in freshwater systems (Woolway et al., 2020; O'Reilly et al., 2015). Increasing surface water temperature is particularly important as it can impact dissolved oxygen availability, timing and composition of algal blooms, and stratification dynamics (Woolway et al., 2020). Lakes and reservoirs around the world have shown warming trends, often outpacing increase in air temperature, especially in temperate and boreal regions (O'Reilly et al., 2015). These changes alter physical habitat conditions and exacerbate existing stressors such as eutrophication with potential synergistic effects on water quality and ecological stability.

Changes in water temperature have been noted across the Great Lakes (Dobiesz & Lester, 2009; McCormick & Fahnenstiel, 1999). In the Great Lakes increasing temperatures have been associated with increasing algal blooms which tend to be HABs (Dobiesz & Lester, 2009, Woolway et al., 2022; Paerl et al., 2011). Increasing water temperatures reduce dissolved oxygen, alter microbial and phytoplankton metabolism, and extend the window for HAB development (Carey et al., 2012; Paerl & Huisman, 2008). This is a concern as climate induced warming may offset progress from reducing phosphorus as well as other management actions. Understanding the role of water temperature in these interactions is essential for effective lake management, particularly in the Severn Sound region where eutrophication is a long-standing concern.

Although trophic status of the Great Lakes, including Lake Huron, has shifted towards oligotrophy (Barbiero et al., 2012), there are concerns that increases in temperature could cause a resurgence in eutrophication and HABs. Lake Huron has experienced increasing water temperature trends which increases the concern of potential impacts of temperature changes (McCormick & Fahnenstiel, 1999). These climatic shifts,

particularly warming water temperatures, are also influencing phytoplankton dynamics. Georgian Bay has seen changes in phytoplankton community composition caused by climate change and the timing and changes have been different across the embayments related to site-specific characteristics (Sivarajah et al., 2018). These findings underscore the importance of considering localized thermal dynamics when assessing ecosystem response to climate change.

1.5 Phytoplankton

Phytoplankton are free-floating microscopic algae that are primarily phototrophic and rely on photosynthesis for growth. Phytoplankton are important primary producers that support higher trophic levels and can influence nutrient availability through uptake and recycling processes. Their abundance, diversity, and community composition can shift dramatically in response to changes in nutrients, temperature, light availability, and grazing pressures (Reynolds, 2006). Phytoplankton are not only integral to ecosystem function but also serve as bioindicators used in environmental monitoring, reflecting shifts in water quality and ecosystem health.

Phytoplankton communities in freshwater systems are composed of a range of taxonomic and functional groups that differ in morphology, nutrient requirements, environmental tolerances, and ecological roles. The main groups observed in Severn Sound include bacillariophytes (diatoms), chlorophytes (green algae), chrysophytes (golden algae), cryptophytes, cyanophytes (cyanobacteria), dinophytes (dinoflagellates), and euglenophytes. These groups exhibit distinct seasonal and spatial patterns that reflect differences in their ecological niches and environmental tolerances. Bacillariophytes have

a cell wall composed of silica and are non-motile that perform best in well-mixed and nutrient-rich waters (Reynolds, 2006). Chlorophytes are a diverse group of phytoplankton with simple cell structures that tend to thrive in eutrophic, well-lit environments and can tolerate a wide range of nutrient conditions (Reynolds, 2006). Chrysophytes are mixotrophic flagellates that can persist in cold, nutrient-poor, and low-light environments. Cryptophytes are cold and low-light tolerant phytoplankton (Reynolds, 2006). Cyanophytes are cosmopolitan prokaryotes that live as unicells or colonies in a range of environments, but can grow well in warm, nutrient-rich, and stratified environments (Reynolds, 2006). Dinophytes are motile phytoplankton that can easily migrate which allows them to move vertically to find access to light and nutrients (Reynolds, 2006). Euglenophytes are a less studied group that is commonly found in nutrient-rich, shallow, and sheltered water, and is tolerant of low oxygen and high organic matter (Reynolds, 2006). Abundance, diversity, and composition of these phytoplankton groups respond differently to changes in nutrients, temperature, mixing, and grazing pressure, thus, phytoplankton are useful indicators for ecological conditions and anthropogenic impacts.

Seasonal succession of phytoplankton is influenced by changes in light, temperature, nutrient availability, and physical mixing (Sommer et al., 1986). Differences in seasonal succession patterns across the Great Lakes have been noted (Munawar & Munawar, 1986). Previously in Lake Huron, bacillariophytes dominated these assemblages regardless of season (Munawar & Munawar, 1986). In spring, the majority of phytoplankton composition was bacillariophytes. In summer through fall bacillariophytes continued to dominate, but cyanophytes and chlorophytes also increased

(Munawar & Munawar, 1986). More current evaluations show bacillariophytes being replaced by chrysophytes, cryptophytes, and dinophytes and summer phytoplankton has a more even distribution of dinophytes, chrysophytes, bacillariophytes (Reavie et al., 2025).

Harmful algal blooms occur when certain algal taxa grow to excessive levels that cause negative impacts in aquatic ecosystems. These blooms can lead to hypoxia during decomposition, disrupt food web dynamics, and diminish water quality for drinking and recreation (Brenckman et al., 2025). Cyanobacteria are a particular concern as they can produce toxins such as microcystins, anatoxins, saxitoxins and cylindrospermopsin (Chorus & Bartram, 1999). Key blooming genera in the Great Lakes and Severn Sound include *Aphanizomenon, Dolichospermum* (formerly *Anabaena*), *and Microcystis.* Both *Dolichospermum* and *Aphanizomenon* are considered diazotrophic, meaning they can fix nitrogen to support growth. Some subgroups of these taxa can produce toxins such as microcystin, anatoxin-a, and saxitoxin (Österholm et al., 2020). *Microcystis* is considered a non-diazotrophic taxon that relies on external sources of nitrogen. It is well known for its production of microcystins, which are harmful toxins to some aquatic organisms, livestock, and humans (Svirčev et al., 2017). Harmful algal blooms can have significant economic, ecological, and human health impacts making them a significant management concern. Timing, frequency, and composition of blooms are important indicators of ecosystem health and eutrophication status and serve as a key focus for management in Severn Sound.

In the mid- to late-1900s, eutrophication was a major concern across the Great Lakes. Severn Sound was listed as an AOC due to chronic eutrophic conditions causing

poor water quality and significant ecological impacts such as habitat degradation. High levels of the key macronutrients phosphorus and nitrogen are widely known to support the excess algal growth associated with eutrophication in surface waters, however, there remains uncertainty on whether nutrient concentration, nutrient ratio, or other drivers control phytoplankton abundance and community composition (Downing et al., 2001; Sakharova et al., 2019; Trimbee & Prepas, 1987). Nutrients that exacerbate eutrophic conditions can be sourced from agriculture, industry, and urban settings (Munawar et al., 2017). Nutrients have been shown to have a stronger effect than temperature on phytoplankton communities during the springtime, however, increases in water temperature have an interactive effect with nutrients that can cause a shift in phytoplankton community composition (Deng et al., 2014).

In addition to nutrients and climate, invasive species have had significant impacts on phytoplankton abundance and community composition in the Great Lakes, especially dreissenid mussels. Zebra and quagga mussels were introduced to the Great Lakes in the mid-1980s to early-1990s (Nalepa & Gauvin). These mussels impact phytoplankton through both highly efficient filter feeding and nutrient recycling. Dreissenid mussels have decreased phytoplankton abundance across the Great lakes as well as shifted community composition (Fahnenstiel et al., 1995; Nicholls & Carney, 2011). These ecological changes are due to the high grazing pressure and selective feeding of dreissenid mussels, which results in increased water clarity and increased HABs (Fisherman et al., 2010; Nicholls et al., 2002; Nicholls & Carney, 2011).

1.6 Nearshore-Offshore zones

In aquatic ecosystems the distinction between nearshore and offshore zones is ecologically and functionally significant (Figure 1.2). The nearshore zone is typically defined as the band or perimeter of a water body between the land and deeper offshore waters that begins at the shoreline and extends to the offshore region (Edsall & Charlton, 1997). Definitions of the nearshore zone vary significantly between studies even within the same waterbody, often guided by specific ecological questions (Kelly, 2009; Yurista et al., 2015). The nearshore includes the biologically important littoral zone, which is the area where light (i.e., photic zone) penetrates to the lake bottom. Light availability in the littoral zone supports photosynthetic growth of aquatic plants and algae. Offshore regions are typically defined based on certain depth or distance from shore, or both.

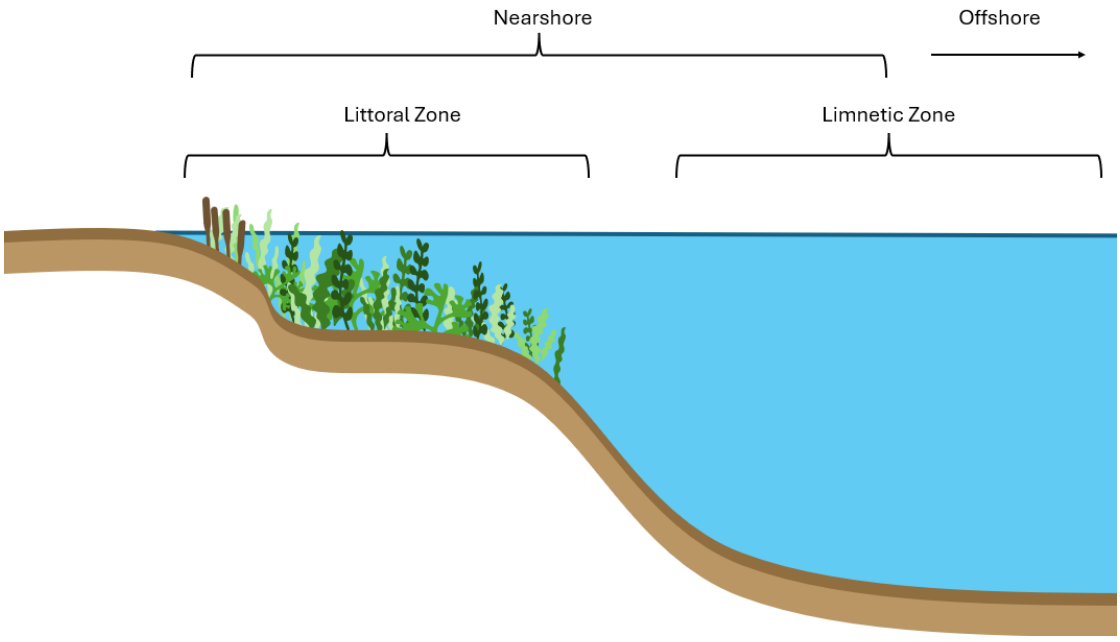

Figure 1.2. Cross-section of a lake showing the spatial characterization of the nearshore-offshore areas. Aquatic plants are relegated to the littoral zone where light can penetrate to the bottom. Phytoplankton can grow in the littoral and limnetic zones but compete with plants for nutrients and light in the littoral zone.

One of the most ecologically important spatial gradients is the distinction between nearshore and offshore zones. Nearshore and offshore areas often display distinct water quality conditions, which can have significant implications for ecosystem processes and management outcomes. These zones differ in depth, hydrodynamics, and exposure to external inputs, which in turn influence water quality and biological communities (Yurista et al., 2016). In general, nearshore areas are shallower and more directly affected by land use activities and tend to exhibit higher concentrations of nutrients, and elevated chlorophyll *a* (Kelly, 2009; Yurista et al., 2016). These nutrient-rich conditions can support elevated chlorophyll *a* concentrations, indicating higher phytoplankton biomass and increased risk of algal blooms, particularly cyanobacteria (Paerl & Otten, 2013; Smith et al., 1999).

Although the offshore is typically defined as depths greater than 30m, this region is significantly shallower, with offshore stations ranging from 2-20 m. Embayment regions like Severn Sound are generally excluded from nearshore-offshore studies (Kelly, 2009; Yurista et al., 2015). Although not following typical nearshore-offshore depth definitions, this research classified sites in a similar fashion, based on proximity to shorelines and depth, allowing for a comparative analysis of spatial variability in water quality. Given the known spatial variability in the sampling regions of Severn Sound (Severn Sound Remedial Action Plan, 1988) these open-water shallow embayment areas where water quality has been traditionally monitored may show distinct differences from the littoral zone.

Understanding these spatial patterns is essential for effective monitoring and management in recovering systems such as Severn Sound. In addition, the nearshore is

typically less frequently monitored in aquatic systems but plays a vital role for aquatic organisms and human use for recreational purposes such as swimming and fishing (Smith & Kirkwood, 2022). Monitoring of the nearshore can offer insights into impacts from land use due to being closer to the point of entry of many inputs. Spatial differences in water quality and phytoplankton composition can inform where and how ecological change is occurring and whether management interventions are having desired effects across habitat types. Examining these zones is important to better capture the complexity of aquatic ecosystems and avoiding generalizations that might arise from single-zone assessments.

1.7 Research goals, objectives, and significance

The overarching goal of my thesis is to enhance understanding of both long-term ecological change and spatial variability in aquatic conditions within Severn Sound, a delisted AOC. This research seeks to evaluate how water quality and phytoplankton communities, have changed over time and how they differ between embayments and the nearshore-offshore areas in Severn Sound. These insights are essential for informing ongoing monitoring and management of Severn Sound as well as remaining AOCs with similar eutrophication related BUIs. Unlike most AOCs in the Great Lakes, the Severn Sound water quality monitoring dataset provides a long-term perspective (almost 50 years) of water quality and phytoplankton shifts and dynamics. Continuous long-term datasets that are consistently collected and span multiple decades are fairly uncommon due to funding and resource constraints, shifting methods and objectives, lacking data

accessibility, and are generally clustered in well-studied regions (Caughlan & Oakley, 2001; Dodds et al., 2012; Ellingsen et al., 2017; Smol, 2019; Wohner et al., 2021).

Therefore, the main goals of my thesis research were to (1) investigate temporal and spatial trends in water quality and phytoplankton communities (both total phytoplankton and cyanobacteria), and (2) assess potential drivers of these changes and differences, particularly as they related to AOC listing and delisting periods. The Severn Sound water quality monitoring dataset offered an exceptional opportunity to evaluate water quality and algal change over three significant time-frames: (1) Before AOC listing (1973-1986); (2) During AOC listing (1987-2003); and (3) Post-AOC delisting (2004-2020 for water quality and 2004-2016 for phytoplankton). To address my research goals, I developed four research objectives and associated hypotheses:

1. Investigate the temporal and spatial variability in water quality within the embayments of Severn Sound, including periods before, during, and after AOC delisting, and identify the environmental drivers underlying these patterns.

   Hypothesis 1: Water quality conditions will show significant improvement from the AOC listing to delisting periods, particularly in nutrients and Secchi depth, reflecting successful remediation efforts.
2. Assess long-term and spatial trends in phytoplankton biovolume and community composition in Severn Sound and determine the key factors influencing these dynamics.

Hypothesis 2: Total phytoplankton biovolume will decline over time, with shifts in community compositions corresponding to reductions in nutrient concentrations and changes in water temperature.

3. Examine temporal and spatial shifts in cyanobacterial community composition and dynamics and evaluate the environmental drivers contributing to these changes in Severn Sound.

   Hypothesis 3: Cyanobacterial community composition will shift over time in response to changes in nutrient levels and water temperature.

4. Assess nearshore water quality in Severn Sound and compare with offshore water quality characteristics.

   Hypothesis 4: Nearshore embayments will exhibit higher nutrient concentrations and more variable water quality conditions than offshore areas.

By exploring long-term water quality, phytoplankton, cyanobacteria and nearshore-offshore water quality across Severn Sound, the following chapters aim to address knowledge gaps related to environmental change in Severn Sound. Chapter 2 investigates how long-term water quality has changed over space and time and identifies important time periods (including those associated with AOC listing and delisting) and environmental drivers of this change. Chapter 3 shows how phytoplankton biovolume and community composition has changed over time and across embayments in Severn Sound, including important time periods of change, and explores important drivers such as nutrients, climate, and invasive species. Chapter 4 focuses on cyanobacterial community dynamics and drivers with a specific focus on HAB-forming taxa (*Dolichospermum*, *Aphanizomenon*, and *Microcystis*) in Severn Sound. Finally, Chapter 5

assesses nearshore-offshore water quality profiles to determine if offshore water quality sampling is comparable to local nearshore conditions. My findings in Chapters 2, 3, and 4 document long-term changes of water quality, phytoplankton, and cyanobacteria in a delisted Area of Concern which can be useful for management of other areas facing similar concerns surrounding eutrophication. My findings in Chapter 5 document concurrent nearshore-offshore conditions across multiple embayments to establish the value of nearshore sampling for capturing ecological condition in the biologically productive littoral zone. Overall, this thesis contributes to the scientific basis for ecosystem management in Severn Sound and similar embayment systems in the Great Lakes, particularly in the context of nutrient management, HABs risks, and climate change.

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Chapter 2. Nearly 50 years of water quality monitoring shows improvements and remaining challenges for a delisted Great Lakes Area of Concern

2.1 Introduction

Severn Sound is a unique 130-km^2 embayment-system located in south-eastern Georgian Bay, Lake Huron on the Canadian side of the Great Lakes. The relatively shallow depths of Severn Sound's embayments (3-20 m), which receive mostly agricultural and urban runoff, have made them susceptible to eutrophication and habitat degradation. Since the mid-1960's, this region has dealt with excessive algal growth that impacted fish habitat and recreational activities such as swimming (Severn Sound Remedial Action Plan, 1993). In 1987, under the Canada-US Great Lakes Water Quality Agreement (GLWQA), Severn Sound was listed as an Area of Concern (AOC) (International Joint Commission, 1978). Severn Sound had six Beneficial Use Impairments (BUIs): eutrophication, degradation of fish and wildlife populations, loss of fish and wildlife habitat, restrictions on fish and wildlife consumption, degradation of aesthetics, and restriction on dredging activities (Severn Sound Remedial Action Plan, 1988). Thus, a Remedial Action Plan (RAP) was formed to address these concerns. This plan for remediation (Severn Sound Remedial Action Plan, 1993) was put forward following documentation of environmental conditions and issues (Severn Sound Remedial Action Plan, 1988). A final report documented how Severn Sound met the delisting objectives for the AOC (Sherman, 2002). The most notable action was nutrient mitigation that targeted point and non-point sources of nutrients (phosphorus being the

main nutrient of concern). The RAP was deemed successful when Severn Sound became delisted in 2003 (Sherman, 2002). With respect to water quality, the following delisting objectives had to be met:

- Total phosphorus concentration < 15 µg/L in open waters and < 20 µg/L in Penetang Harbour
- Chlorophyll *a* concentration < 5 µg/L in open waters and < 7 µg/L in Penetang Harbour
- Water clarity (Secchi depth) > 3 m (or on bottom) in open waters and > 2 m (or on bottom) in Penetang Harbour
- Annual minimum bottom water dissolved oxygen concentration > 5 mg/L

Eutrophication of Severn Sound, though much improved since it was first listed as an AOC, continues to be a concern. Reductions in phosphorus and chlorophyll a concentrations attributed to RAP mitigation measures for Severn Sound in the mid 1990s also occurred around the same time as the zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussel invasion of Lake Huron (Cha et al., 2011; Johengen et al.,1995). Secchi depth also increased at this time across Lake Huron, with an increase in variability between nearshore and offshore sites as well as across seasons (Binding et al., 2015; Dove & Chapra, 2015). In combination, reduced phytoplankton biomass and improved water clarity are typically associated with the intense filtering pressure of dreissenid mussels (Fahnenstiel et al., 2010). However, due to a lack of consistent long-term surveys of dreissenid mussels in Severn Sound, it can only be

inferred that they played a role in the notable water quality changes that happened in the mid-1990s.

Increasing water temperatures are linked to increased harmful cyanobacteria algal blooms (Moss et al., 2011; O'Neil et al., 2012), and this is likely also occurring in Severn Sound based on results of algae sampling and the increasing number of nuisance algae reports received by the Severn Sound Environmental Association (SSEA). The growing dominance of cyanobacteria under increasing temperature scenarios is a concern, especially since their growth rates are optimized (Robarts & Zohary, 1987; Paerl & Paul, 2012). Increases in water temperature have been seen across the Great Lakes, including Lake Huron (Dobiesz & Lester, 2009; McCormick & Fahnenstiel, 1999). Air temperature can be used to predict changes in water temperature across the Great Lakes (Trumpickas, 2009), thus as climate change continues to cause increases in air temperature, we will likely continue to see increases in water temperature across Lake Huron which could facilitate more frequent bloom conditions.

This study aims to investigate the long-term water quality patterns and trends in the delisted AOC Severn Sound over an almost 50-year period (1973-2020). I aim to (1) assess spatial trends and differences in the four embayments of Severn Sound during the time period studied, (2) investigate changes in water quality patterns at important time periods, including the implementation of nutrient reduction strategies and before and after the introduction of the invasive dreissenid mussels, and (3) assess the role of climate change on shifts in water quality in Severn Sound. Using data provided by the SSEA, I applied an array of statistical approaches, including Generalized Additive Mixed Models

(GAMM), to elucidate trends and relationships between parameters, as well as overall changes in long-term water quality conditions across Severn Sound.

2.2 Methods

2.2.1 Data collection

The Ministry of the Environment began collecting water quality and temperature data annually in 1973 following an initial survey in 1969, and this work was continued by the SSEA beginning in 1997 using the same methods (Severn Sound Environmental Association, 2022). Water samples were collected as depth integrated composites from surface to twice the Secchi depth or 1 m off bottom, whichever was less. Temperature was recorded using a multi-parameter sonde at 1 m depth intervals from surface to 1 m off bottom. For the purpose of this study, temperature at 1 m below surface was used for statistical analyses. This study investigated data from 1973-2020 for 5 sites, P1, P4, M1, BS, PM2 (Figure 2.1). Data was generally collected biweekly from May to October, but dates and frequency of collection varied somewhat by year and site. Due to inconsistency of sample collection, only data from May-September was included in analyses. From 1969-1985, water temperature data was only available digitally as monthly average temperature from May-September. Starting in 1986, biweekly data was available. Collection of chlorophyll *a* data was essentially discontinued due to shortages in lab resources after 2008 and thus, statistical analyses only include data until this time.

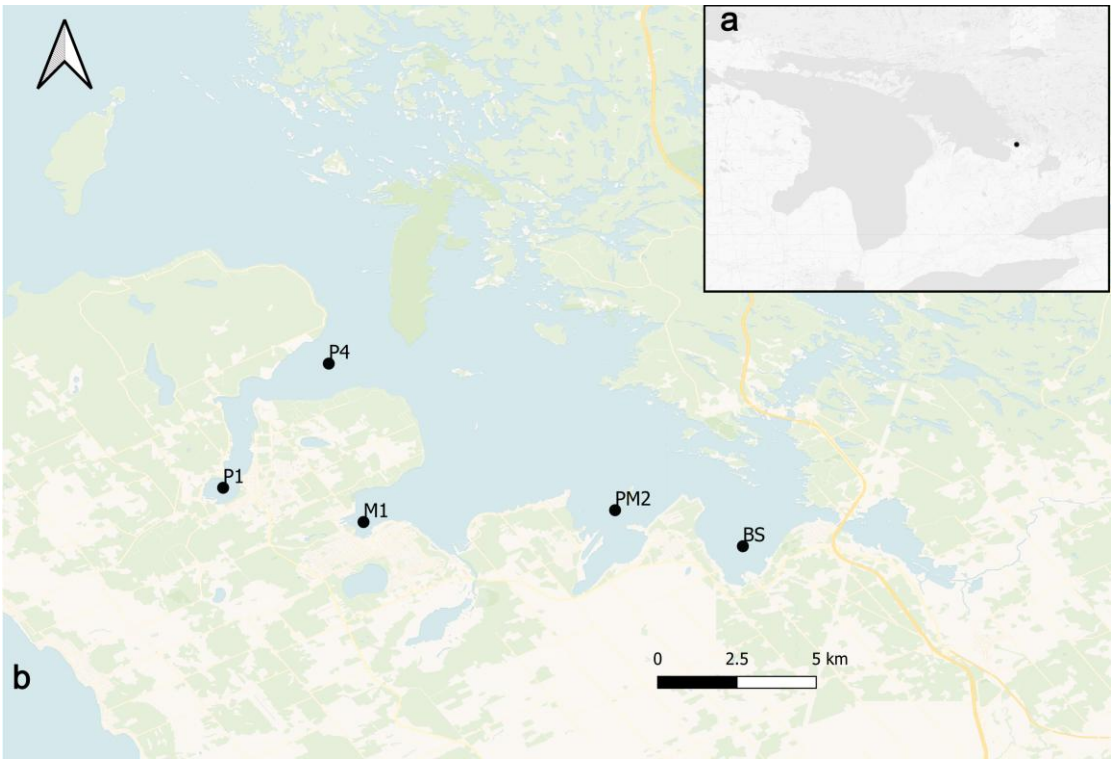

Figure 2.1. Location of long-term sampling sites in Severn Sound, Lake Huron. Map a) shows location of Severn Sound in Lake Huron. Map b) shows sampling locations, stations P1 and P4 are located in Penetang Harbour, station M1 is located in Midland Bay, PM2 is located in Hogg Bay, and station BS is located in Sturgeon Bay.

Parameters that were consistently sampled across all long-term sites were investigated in this study: total chlorophyll *a* (Chla) (µg/L), ammonia + ammonium (TAN, sum of NH_3 and NH_{4+}) (µg/L), nitrate + nitrite (TNN, sum of NO_{3-} and NO_{2-}) (µg/L), total organic nitrogen (TON, Total Kjeldahl Nitrogen subtract TAN) (µg/L), total nitrogen (TN) (µg/L), total phosphorus (TP) (µg/L), Secchi disk visibility (Z_{SD}) (m), and water temperature (WT) (°C). It should be noted that on some dates in some years at P1 and BS, Z_{SD} may be less accurate due to site shallowness and aquatic vegetation density. These data points likely add variability to the dataset. Samples were processed by the Ontario Ministry of Environment, Conservation and Parks labs in Rexdale and Dorset

using standard analytical methods, including low level phosphorus analysis at the Dorset lab. Over the study period, changes in analytical methods have occurred (e.g. TP, Chla) and these were accounted for to the extent possible.

2.2.2 Data processing

In general, the water quality parameters collected did not follow normal distributions even with common transformations, so non-parametric statistical analyses were conducted when appropriate. All statistical analyses were performed in the open-sourced software R version 4.4.0 (R Core Team, 2024). A Friedman's Analysis of Variance (ANOVA) was used for repeated measures at each station with a Bonferroni post hoc test to determine if water quality parameters differed between sites (Friedman, 1937; Wilcoxon, 1945). Since the data were collected at the five stations on the same day, a pairwise comparison was used to compare data between sites. The ANOVA was run in R using the R package *rstatix* (Kassambara, 2023). A Spearman Correlation Matrix was run using the *corrplot* package in the R statistical software to determine the relationship between all water quality parameters (Wei & Simko, 2024). The Correlation Matrix was run using data at each site, and data was pooled across the stations to compare relationships between parameters across Severn Sound. A Principal Component Analysis (PCA) was used to determine covariation of water quality parameters and to determine differences of covariation across sites using the R package *ggfortify* (Horikoshi & Tang, 2016). Data was pooled into a yearly average using May-September data for each parameter to run a Mann Kendall using the *Kendall* package in the R statistical software to determine overall trends in water quality over the time frame studied (McLeod, 2022).

Due to the non-linear nature of the data, GAMM were created using the *mgcv* package in the R statistical software (Wood, 2011). This analysis allowed us to identify significant time periods of change in water quality. All models utilized the tweedie family. Model building followed a process of first checking for significance of Year and Day of Year (DOY), then checking for significance of station. For all models, year, DOY, and station were significant, and then any parameters that were potentially explanatory were checked for significance. If parameters were not shown to be significant, they were removed from the model and the Akaike Information Criterion (AIC) (Akaike, 1998; Pearce et al., 2011; Zirkle, 2016) was checked for improvement. After the most suitable model was found, the model was checked for impacts from auto regressive moving averages (ARMA). If this improved the model then this was the chosen model; if it did not improve the model, then the previous model was chosen.

Model 1 = s(Year) + s(DOY)

Model 2 = s(Year) + s(DOY) + Station

Model 3 = s(Year) + s(DOY) + Station + s(Relative Parameters)

Model 4 = s(Year) + s(DOY) + Station + s(Relative Parameters) + ARMA (if relevant)

2.3 Results

When investigating statistically significant correlations between water quality parameters, I found that overall relationships were similar across the five stations, however, the strength of correlation did vary across the stations (Figure 2.2). Due to a lack of Chla data after 2008, two PCAs were constructed to investigate correlations between water quality parameters and differences among sites. When including Chla data, the first principal component (PC1) explained 36.15% of the variance, while the second principal component (PC2) explained 23.03% (Figure 2.3a). There was a strong correlation between Chla and TP, and a strong correlation between TAN and TON. These four parameters were all positively (moderately) correlated and were all moderately negatively correlated with Z_{SD}. TN and TNN have a moderately positive correlation and are both negatively correlated with WT. Station P1 had the most variability in its water quality conditions and was the least similar to other sites. The four other stations had more overlap in their water quality conditions and had overall less variability. The second PCA included the full timeframe without Chla to determine if the data collected post-2008 had different patterns and relationships. However, this PCA was comparable to the first PCA, where axis 1 explained 35.7% of the variance and axis 2 explained 26.66% of the variance (Figure 2.3b). Although correlation was similar across stations, the majority of the water quality parameters were significantly different across stations (ANOVA, p-value <0.05) (Table 2.1A, Table 2.1B).

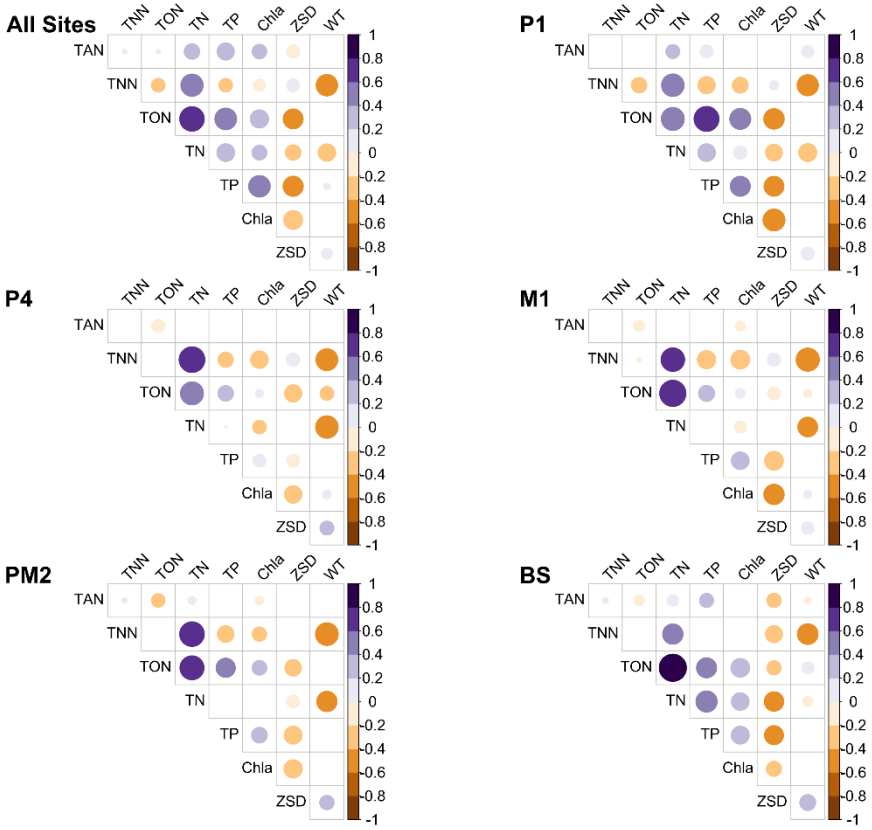

Figure 2.2. Correlation matrices of water quality parameters from May-September 1973-2020 with only significant relationships shown (p-value <0.05). Size and colour indicate strength of relationship. Pooled data from all sites, P1, P4, M1, PM2, and BS.

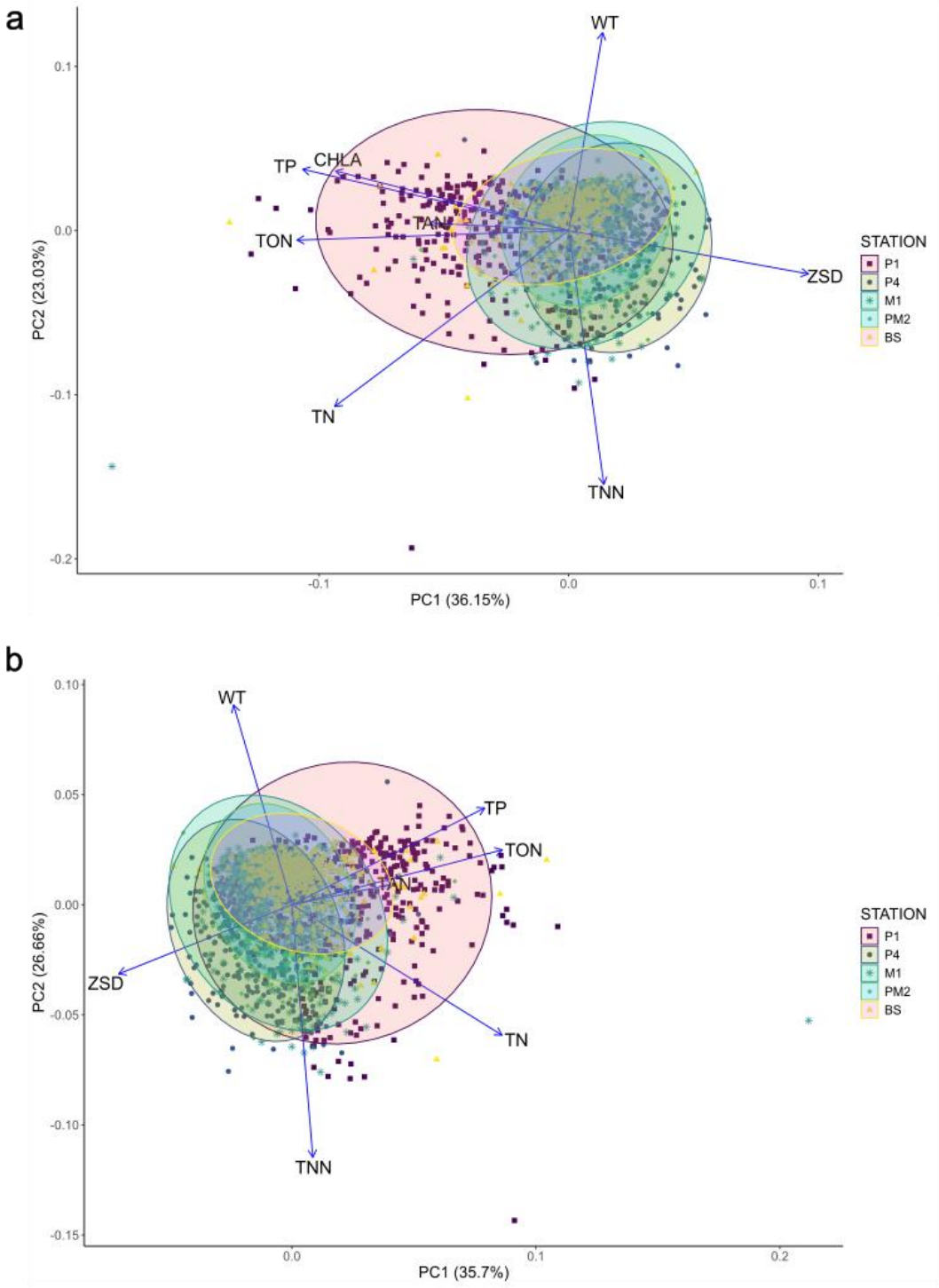

Figure 2.3. Principal Component Analysis of water quality parameters with data from May-September 1973-2008 including Chla (a) and with data from 1973-2020 without Chla (b).

Table 2.1A. Comparison of water quality data between Severn Sound stations with the post hoc Bonferroni test. The Friedman test had a p-value of <0.05. All significant p-values (<0.05) are bolded.

			TAN		TNN		TON		TN	
		n	418		415		413		411	
Site 1	Site 2		Sum of signed ranks	P-value	Sum of signed ranks	P-value	Sum of signed ranks	P-value	Sum of signed ranks	P-value
P1	BS		6848	**<0.05**	3789	**<0.05**	48071	0.102	12424	**<0.05**
P1	P4		76503	**<0.05**	24628	**<0.05**	80533	**<0.05**	80747	**<0.05**
P1	PM2		77556	**<0.05**	53290	**<0.05**	66976	**<0.05**	81866	**<0.05**
P1	M1		5988	**<0.05**	32309	1	9027	**<0.05**	4030	**<0.05**
P4	BS		43384	**<0.05**	795	**<0.05**	82838	**<0.05**	56969	**<0.05**
P4	M1		51987	**<0.05**	11270	**<0.05**	72467	**<0.05**	55259	**<0.05**
P4	PM2		25356	**<0.05**	79570	**<0.05**	6261	**<0.05**	45264	**<0.05**
M1	BS		33085	0.52	1590	**<0.05**	79411	**<0.05**	48726	**<0.05**
M1	PM2		39513	0.086	60348	**<0.05**	20207	**<0.05**	59050	**<0.05**
PM2	BS		34778	1	5435	**<0.05**	79813	**<0.05**	64879	**<0.05**

Table 2.1B. Continuation of the comparison of water quality data between Severn Sound stations with the post hoc Bonferroni test. The Friedman test had a p-value of <0.05. All significant p-values (<0.05) are bolded.

			TP		Chla		Z_{SD}		WT	
		n	328		416		437		456	
Site 1	Site 2		Sum of signed ranks	P-value	Sum of signed ranks	P-value	Sum of signed ranks	P-value	Sum of signed ranks	P-value
P1	BS		7582	**<0.05**	3571	**<0.05**	50250	**<0.05**	63599	**<0.05**
P1	P4		85168	**<0.05**	49549	**<0.05**	390	**<0.05**	84757	**<0.05**
P1	PM2		81419	**<0.05**	49763	**<0.05**	13190	**<0.05**	40998	**<0.05**
P1	M1		1676	**<0.05**	3741	**<0.05**	79738	**<0.05**	35273	**<0.05**
P4	BS		72319	**<0.05**	20031	0.077	1570	**<0.05**	87177	**<0.05**
P4	M1		68579	**<0.05**	36634	**<0.05**	4968	**<0.05**	82410	**<0.05**
P4	PM2		7140	**<0.05**	26994	0.407	83362	**<0.05**	6961	**<0.05**
M1	BS		51929	**<0.05**	14487	**<0.05**	10695	**<0.05**	73143	**<0.05**
M1	PM2		30610	**<0.05**	37409	**<0.05**	61591	**<0.05**	23594	**<0.05**
PM2	BS		47536	**<0.05**	19487	**<0.05**	21979	**<0.05**	60240	**<0.05**

Due to the long-term duration of data collection, it is important to look at both the overall changes in water quality parameters and when these changes happened (Figure A1, Figure A2). Total Ammonia Nitrogen (TAN) had no significant overall trends (Table 2.2). Both TN and WT had a significant decrease (Mann Kendall, p-value < 0.05) at station P1. Secchi Disk Visibility (Z_{SD}) increased significantly at stations P1 and BS. Parameters TNN, TON, and Chla had a significantly increasing trend at all stations, excluding BS. Total Phosphorus (TP) significant decreased at all stations.

Table 2.2. Mann-Kendall analysis performed on yearly averages of water quality parameters for each station in Severn Sound from 1973-2020, with the exception of Chla which was performed from 1973-2008 due to data availability.

Parameter	Statistic	Station				
		P1	P4	M1	PM2	BS
TAN	Tau	-0.13	0.02	-0.01	0.06	0.18
	P-value	0.22	0.85	0.96	0.55	0.08
TNN	Tau	0.5	0.34	0.39	0.24	0.07
	P-value	**<0.05**	**<0.05**	**<0.05**	**<0.05**	0.49
TON	Tau	-0.61	-0.38	-0.38	-0.31	-0.17
	P-value	**<0.05**	**<0.05**	**<0.05**	**<0.05**	0.1
TN	Tau	-0.34	-0.08	-0.01	-0.19	-0.11
	P-value	**<0.05**	0.43	0.9	0.06	0.29
TP	Tau	-0.67	-0.59	-0.6	-0.64	-0.52
	P-value	**<0.05**	**<0.05**	**<0.05**	**<0.05**	**<0.05**
Chla	Tau	-0.38	-0.46	-0.42	-0.47	-0.08
	P-value	**<0.05**	**<0.05**	**<0.05**	**<0.05**	0.49
ZSD	Tau	0.24	0.012	0.12	0.14	0.24
	P-value	**<0.05**	0.91	0.23	0.16	**<0.05**
WT	Tau	0.39	0.16	0.19	0.16	0
	P-value	**<0.05**	0.11	0.06	0.1	0.17

I evaluated long-term water quality trends across all parameters using Generalized Additive Mixed Models to determine significant explanatory variables over time. All water quality parameters improved with the inclusion of year, DOY, and station, but varied as to which other water quality parameters or if ARMA improved their model (Table 2.3, Figure 2.4 and 2.5). The TAN GAMM with the lowest AIC value included year, DOY, and station and used a moving average of 2 (R^2 adjusted = 0.43) (Table A1, Table A2). The GAMM of TNN with the lowest AIC value included year, DOY, and station and used a moving average of 1 (R^2 adjusted = 0.62) (Table A3, Table A4). The TON model with the lowest AIC value included year, DOY, and station and used an autoregressive component of 1 (R^2 adjusted = 0.35) (Table A5, Table A6). The GAMM of TN with the lowest AIC value included year, DOY, and station ($p<0.05$) and used an autoregressive component of 2 (R^2 adjusted = 0.44) (Table A7, Table A8). The TP model with the lowest AIC included year, DOY, station, and parameter: WT ($p<0.05$) and used a moving average of 2 (R^2 adjusted = 0.55) (Table A9, Table A10). The Chla GAMM with the lowest AIC value included year, DOY, station, and parameters: TP, TON, TAN, TNN ($p<0.05$) and utilized a moving average of 1 (R^2 adjusted = 0.53) (Table A11, Table A12). The GAMM of Z_{SD} that had the lowest AIC included year, DOY, station, and parameter: Chla ($p<0.05$) and utilized a moving average of 2 (R^2 adjusted = 0.63) (Table A13, Table A14). The WT model with the lowest AIC value included year, DOY, and station ($p<0.05$) and used an autoregressive component of 1 (R^2 adjusted = 0.82) (Table A15, Table A16).

Table 2.3. Best Generalized Additive Mixed Model for each parameter investigated. Final model included year, DOY, station, significant water quality explanatory variables, and autoregression and moving averages if they improved model AIC.

Parameter	Final Model	R^2
TAN	TAN ~ s(YEAR, k=47) + s(DOY, k=15) + STATION, correlation = corARMA(form = ~1|YEAR, q=1)	0.43
TNN	TNN ~ s(YEAR, k=47) + s(DOY, k=15) + STATION, correlation = corARMA(form = ~1|YEAR, q=1)	0.62
TON	TON ~ s(YEAR, k=47) + s(DOY, k=15) + STATION, correlation = corARMA(form = ~1|YEAR, p=1)	0.35
TN	TN ~ s(YEAR, k=47) + s(DOY, k=15) + STATION + s(WT), correlation = corARMA(form = ~1|YEAR, p=2)	0.44
TP	TP ~ s(YEAR, k=47) + s(DOY, k=15) + STATION +s(WT), correlation = corARMA(form = ~1|YEAR, q=2)	0.55
Chla	Chla ~ s(YEAR, k=36) + s(DOY, k=20) + STATION + s(TP)+ s(TON) + s(TAN) + s(TNN), method="REML", family=tw, correlation = corARMA(form = ~1|YEAR, q=1)	0.53
Zsd	ZSD ~ s(YEAR, k=36) + s(DOY, k=15) + STATION + s(Chla), correlation = corARMA(form = ~1|YEAR, q=2)	0.63
WT	WT ~ s(YEAR, k=47) + s(DOY, k=15) + STATION, correlation = corARMA(form = ~1|YEAR, q=2)	0.82

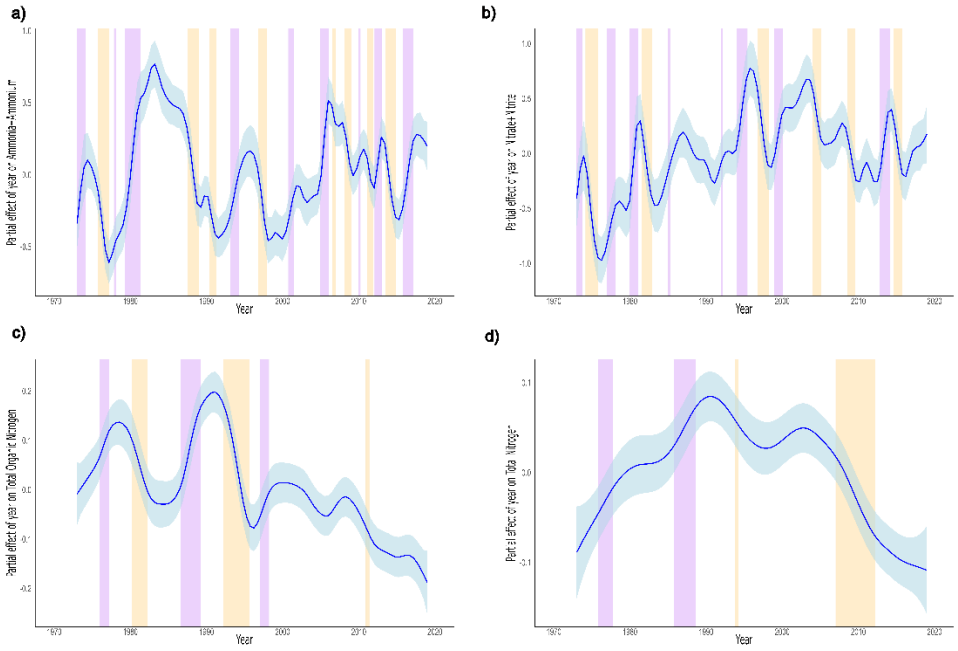

Figure 2.4. Partial effects plot of a) TAN, b) TNN, c) TON, d) TN in Severn Sound from 1973-2020 with the blue ribbons indicating the 95% confidence intervals, orange bars indicating areas of significant decrease and purple bars indicating areas of significant increase based on the first derivative of the model term.

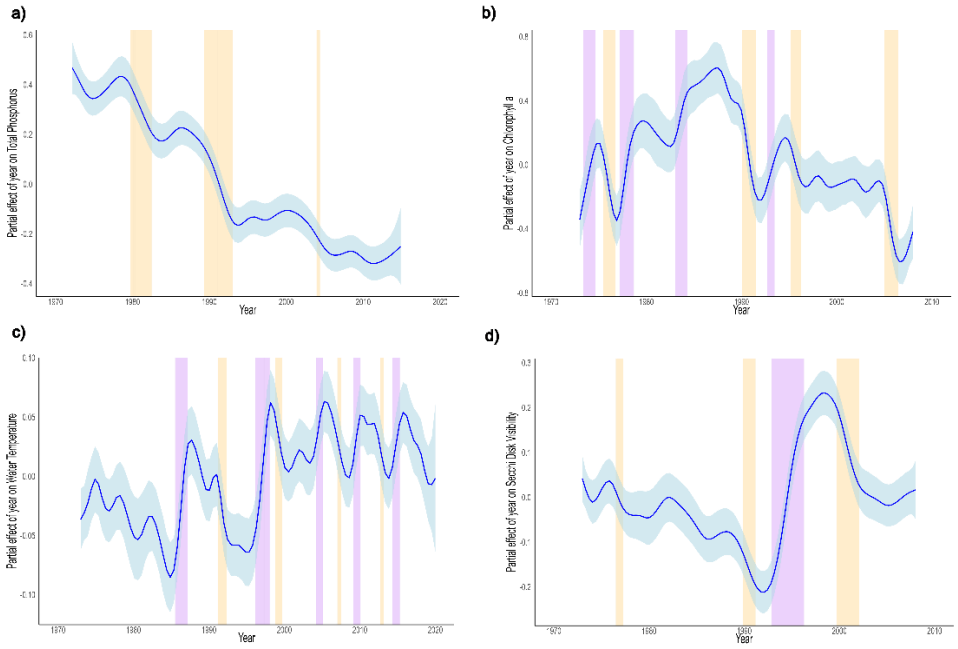

Figure 2.5. Partial effects plot of a) TP, b) Chla, c) WT, d) Z_{SD} in Severn Sound from 1973-2020 (a, c) and 1973-2008 (b, d) with the blue ribbons indicating the 95% confidence intervals, orange bars indicating areas of significant decrease and purple bars indicating areas of significant increase based on the first derivative of the model term.

2.4 Discussion

These findings revealed that the SSEA's long-term stations have unique water quality conditions. This indicates that site-specific conditions rather than large scale mixing across Severn Sound likely drives water quality in each embayment. Even so, overall trends were similar across water quality parameters, but some sites experienced more changes than others. For example, station P1 differed the most from other stations, including a second station (P4) that is within the same embayment, but closer to the open-water area of Severn Sound. The unique water quality conditions of P1 is likely driven in part by its notable morphometric differences compared to the other stations (Severn Sound Remedial Action Plan, 1988). The entrance to Penetang Harbour is constricted which limits mixing with the rest of Severn Sound, whereas the other sites are more open to water exchange, especially P4, which is directly adjacent to the open-water area. As a result, the other stations generally have lower nutrient levels compared to P1.

In other studies, within-lake water quality variation has largely been attributed to site-specific differences in lake morphometry and basin characteristics (Pla, 2005). Additionally, P1 had more significant changes in water quality parameters over time, such as Z_{SD}, WT, and TN, when comparing yearly averages. This may be due to the proximity of P1 to the nearshore zone, the shallow depth (<3 m) and the fact that there are two wastewater treatment plants in the vicinity that both underwent significant upgrades resulting in reduced nutrient loading. Other studies that found an increased difference in nearshore and offshore chlorophyll *a* concentrations in Lake Huron and Michigan due to nutrient loading to the nearshore as well as dreissenid filtering and nutrient resuspension (Stadig et al., 2020).

Overall reduction of TP and phytoplankton blooms were major objectives of the Remedial Action Plan to demonstrate reduced eutrophication in Severn Sound. Total phosphorus levels significantly decreased during the study period, and Chla declined at all stations except BS. This is likely due to initial lower levels of Chla related to the high density of aquatic vegetation outcompeting algae at BS (Severn Sound Remedial Action Plan, 1988). There were two notable periods of significant decline in TP during the 1980s and 1990s, respectively. The decrease in the 1980s is likely related to actions implemented under the GLWQA, as many areas around the Great Lakes were subjected to nutrient reduction programs aimed at reducing point-source nutrient loadings (Stadig et al., 2020). According to the Severn Sound Remedial Action Plan (1988), there were sewage plant upgrades in Severn Sound during this period. Saginaw Bay in Lake Huron also had a decrease in phosphorus levels that were linked to upgrades in the sewage treatment as well as the phosphorus detergent ban (Bierman et al., 1984). Secchi depth visibility (Z_{SD}) also improved during the 1980s, however, Chla levels continued to rise. The study in Saginaw Bay found a lack of response in Z_{SD} and a poor correlation between phosphorus and Chla that was likely due to wave action causing sediment resuspension (Bierman et al., 1984).

The significant increase in Z_{SD} and decrease in TP and Chla in the 1990s is likely in part due to the introduction of invasive dreissenid mussels, which were first reported in Lake Huron in 1990 (Nalepa et al., 1995). Due to their effective filtration abilities and benthic diversion of phosphorus (i.e., the nutrient shunt), dreissenid mussels are known to increase water clarity by decreasing Chla and suspended sediment in invaded ecosystems, with resulting decreases in TP (Cha et al., 2011; Budd et al., 2001; Hecky et al., 2004;

Nalepa et al., 1995). Similar to other areas in Lake Huron, Dobiesz and Lester (2009) found that the Georgian Bay basin was experiencing a subtle (non-significant) decrease in Z_{SD} before the arrival of invasive dreissenid mussels, whereas after invasion, there was a significant increase in Z_{SD}. In addition, Z_{SD} increased at sites P1 and BS, but not P4, M1, or PM2 which could be due to specific site characteristics (i.e., shallow depth at P1 and BS) where Secchi disk would sometimes reach the lakebed or be obscured by aquatic vegetation.

In contrast to TP, total nitrate nitrogen (TNN) increased across most sites in Severn Sound over the study period. This may be related to similar TNN trends observed in tributaries across the Great Lakes basin where row-crop systems have increased in density (DeBues et al., 2019; Liu et al., 2022). Even though TNN increased over the study period, total nitrogen (TN) did not appreciably change with the exception of P1, which had decreasing levels. Total organic nitrogen (TON) decreased across all sites except BS. Total Nitrogen in Severn Sound followed a very similar trend seen in a river mouth leading into Lake Erie where TN increased into the 1990s and then decreased afterward (Stow et al., 2015). Although phosphorus is generally a limiting nutrient for algal growth, increased nitrogen levels can also increase algae growth including harmful algal blooms (Paerl, & Otten, 2013). In addition, high nitrate levels can increase microcystin producing populations of *Microcystis aeruginosa* (Yoshida et al., 2007). This could be a concern if the increased levels of TNN cause increased populations of toxic algae in Severn Sound.

The GAMM for WT has some periods of significant increase and shows an increase in temperature from 1973 to 2020. However, the Mann Kendall analysis only

shows an increase in water temperature at station P1. This station has less mixing with the open water which could make it more susceptible to increasing air temperatures than the other stations (Severn Sound Remedial Action Plan, 1988). In addition, the GAMM shows a decrease in water temperature from the start of data collection to the mid-1980s which may mask potential increases. Water temperature trends in the Great Lakes have been variable, with some areas showing increases in temperature and others not (Dobiesz & Lester, 2009; McCormick & Fahnenstiel, 1999). Overall surface water temperature in Lake Huron has increased in August, but when looking at basins separately, Georgian Bay did not increase (Dobiesz & Lester, 2009). In addition, pooling of May to September temperature data may mask differences in seasonal changes in WT in Severn Sound. Future work could delineate seasonal trends in WT across the long-term monitoring sites.

The findings of this study highlight the distinct water quality conditions of long-term monitoring stations in Severn Sound. Differences among stations that are spatially close are likely due to morphometric differences in the embayment that cause reduced mixing with the open waters. This illustrates the importance of continued monitoring across these stations to capture the full variability in water quality and the need for localized management strategies to address different water quality conditions. The changes seen within Severn Sound are likely due to multiple factors. Long-term changes in water quality have been seen across the Great Lakes due to implementation of the GLWQA and reduction in nutrient loadings. As an AOC, significant effort was put into decreasing nutrient inputs into Severn Sound by improving sewage treatment and reducing agricultural inputs. This is clearly reflected in the long-term dataset used in this study, which captures trends before, during, and after key remediation efforts, offering a

rare opportunity to assess ecosystem response across the full delisting timeline. The introduction of invasive dreissenid mussels likely influenced some changes in nutrient status indicators, specifically Z_{SD} and also likely Chla, although the time-limited Chla dataset (up to 2008) does not show trends as clearly. Even so, dreissenid mussels are known to impact phytoplankton community composition (Fisherman et al., 2010), even if total biomass is not overtly changed. Another interesting find was that change in water temperature was not seen across the entire region when looking at overall trends from the Mann Kendall, however, the GAMM does show that surface water temperature has increased over the study period. Due to previous eutrophic conditions and the link between eutrophication and increased temperature, it is important to continue monitoring water temperature changes and the focus of management strategies to reduce impacts from climate change.

2.5 References

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Chapter 3. Long-term (1973-2016) trends and shifts in phytoplankton communities before, during, and post delisting of a Great Lakes Area of Concern

3.1 Introduction

Phytoplankton are important primary producers in lake ecosystems that also serve as sentinels of environmental change due to their high turn-over rates in response to shifting environmental conditions. Phytoplankton abundance and community structure are influenced by many environmental components. Key nutrients such as phosphorus and nitrogen are well known to impact abundance and community structure (Deng et al., 2014; Trimbee & Prepas, 1987). Higher nutrient levels in water bodies are strongly associated with increased phytoplankton abundance due nutrient availability limiting their productivity (Baer et al., 2023; Frenken et al., 2023). Phosphorus commonly being a limiting nutrient for phytoplankton, was a major target in nutrient reduction programs to reduce algal blooms across the Great Lakes (Bierman et al., 1984; International Joint Commission, 1978). This reduction in nutrient loading was responsible for reduction in phytoplankton abundance across the Great Lakes region (Nicholls et al., 1977, Nicholls 2002; Winter et al., 2011). Changes in nutrient availability and nutrient ratios can also impact phytoplankton community structure and diversity, which has been seen across the Great Lakes region (Baer et al., 2023; Bierman & Dolan, 1981; Frenken et al., 2023; Kovalenko et al., 2017).

In addition to bottom-up controls such as nutrients, top-down controls from the food web also impact phytoplankton abundance and community composition. A major influence of this in the Great Lakes was the introduction of the invasive zebra mussels

(*Dreissena polymorpha*) in the mid 1980 to early 1990s (Nalepa & Gauvin, 1988; Nalepa et al., 1995). These invasive mussels have impacted phytoplankton both indirectly through impacts to nutrient cycling as well as direct impacts from filter feeding. Zebra mussels sequester nutrients for growth, as well as return nutrients to the water column through defecation, including pseudofeces (Arnott & Vanni, 1996; Cha et al., 2011; Vanderploeg et al., 2002). Dreissenid mussels also have direct impacts on phytoplankton causing decreased phytoplankton abundance across the Great Lakes (Fahnenstiel et al., 1995; Nicholls & Carney, 2011; Nicholls & Hopkins 1993). Phytoplankton community composition has shifted due to the selective grazing pressure of dreissenid mussels, but also from dreissenid ecosystem engineering including changes in nutrient form and availability, increased water clarity, and increased occurrence of harmful algal blooms (e.g., *Microcystis aeruginosa*) (Bierman et al., 2005; Fisherman et al., 2010; Nicholls et al., 2002; Nicholls & Carney, 2011).

Although nutrients tend to have a stronger influence on phytoplankton abundance and community composition (Deng et al., 2014; Filiz et al., 2020), climate, land-use, and lake morphology can impact abundance and community directly as well as indirectly through impacts to nutrient and water quality patterns (Peng et al., 2021; Wu et al., 2023). Increased water temperature can decrease phytoplankton diversity and increase cyanobacteria populations and can also have interactive effects with nutrients that can enhance shifts in phytoplankton community composition (Deng et al., 2014; Filiz et al., 2020). Changes in land use, particularly agricultural practices, can influence nutrient inputs into waterways and have participated in conditions causing algal blooms within Lake Erie (Arbuckle & Downing, 2001; Michalak et al., 2013; Wu et al., 2023). Lake

morphological characteristics such as depth, area, and volume can influence phytoplankton community composition through biogeochemical processes, increased light, and changes to habitat (Cardoso et al., 2017; Kolada, 2014; Qui et al., 2020; Wu et al., 2023)

In 1987, as part of the binational GLWQA, the International Joint Commission identified 43 AOC throughout the Great Lakes based on a high degree of environmental degradation (International Joint Commission, 1978). Severn Sound was one of the AOC sites listed due to eutrophication as well as other BUIs (International Joint Commission, 1978). Severn Sound is an approximately 130km^2 embayment system in Georgian Bay, Lake Huron Ontario. Excessive algal growth had been a concern in Severn Sound since the mid 1960s (Severn Sound Remedial Action Plan, 1988). This algal growth and degraded water quality had negative impacts on recreational usage as well as influenced shifts in fish community composition, such as a decline in the walleye population (Severn Sound Remedial Action Plan, 1988).

Phosphorus was identified as a key nutrient causing the excessive algal growth with both point (e.g., sewage treatment facilities) and non-point sources (e.g., agricultural and urban run-off). Reducing phosphorus levels was a major goal towards delisting Severn Sound. The SSEA, local governments, and community stakeholders identified sources of nutrient pollution leading to high levels of eutrophication and together implemented solutions to reduce the nutrient levels (Severn Sound Remedial Action Plan, 1988). A RAP was created to address nutrient pollution, eutrophication, and other BUIs which included delisting objectives such as decreasing phosphorus and Chlorophyll *a* concentrations, increased water clarity, and meet a minimum bottom water dissolved

oxygen concentration (Severn Sound Remedial Action Plan, 1993). When the delisting objectives were met, a final report documented the success (Sherman, 2002) and in 2003, Severn Sound became the second Canadian AOC to be delisted (Canada Water Agency, 2024).

This study aimed to investigate the phytoplankton community in Severn Sound, Ontario over 43 years (1973-2016). My key study objectives were to determine: (1) spatial and temporal changes to total phytoplankton biovolume, (2) spatial and temporal changes to the phytoplankton community composition, and (3) potential drivers of this change including water quality, the inferred introduction of invasive dreissenid mussels, and the role of climate change. I utilized data provided by SSEA and statistical approaches such as RDA (Redundancy Analysis), PERMANOVA (permutational analysis of variance), and GAMM to evaluate differences and changes in total phytoplankton biovolume and the phytoplankton community across the Severn Sound region. This study highlights important drivers of eutrophication in a previous Area of Concern and how phytoplankton levels and profiles have changed with the status of restoration.

3.2 Methods

3.2.1 Data collection

Phytoplankton, water quality, and water temperature data collected by the Severn Sound Environmental Association and the Ontario Ministry of the Environment from 1973 to 2016 were included in data analyses (Severn Sound Environmental Association, 2022a; Severn Sound Environmental Association, 2022b). The five sampling sites

presented in this chapter are the same as in Chapter 2 (Figure 2.1). Environmental parameters including TAN, TNN, TON, TN, TP, Chla, Z_{sd}, and WT were collected as discussed in Chapter 2 methods. Phytoplankton samples were collected on individual dates during the sampling season as depth integrated composites from surface to twice the Secchi depth or 1 m off bottom, whichever was less, matching water quality sampling. Samples were collected as integrated samples using a narrow mouth open bottle from 1973-1999 and an integrator cap from 2000-2016 and preserved using Lugol's iodine solution. Phytoplankton samples were pooled from the entire season and counted as a composite representing the annual seasonal mean. Phytoplankton data was only available up to 2016; thus, analyses were restricted to this time range.

3.2.1 Data processing

Since phytoplankton biovolume was collected as a pooled seasonal sample, water quality data was averaged across the sampling season to align with phytoplankton data. Total phytoplankton biovolume was obtained by summing all phytoplankton samples collected at each site for each sampling year. Phytoplankton division data was analyzed similarly, by pooling phytoplankton samples collected at each site during each sampling year within each division.

Statistical analyses were performed in the open-sourced software R version 4.4.0 (R Core Team, 2024). In general, the water quality and phytoplankton data did not follow normal distribution even with common transformations, thus non-parametric analyses were utilized. Two PERMANOVA's were used to investigate statistical differences in the phytoplankton community across the five stations. One PERMANOVA investigated differences in the phytoplankton community during different AOC designations: Before

AOC designation (1973-1986), during AOC designation (1987-2002) and after delisting of AOC status (2003-2016). Another PERMANOVA investigated changes from the zebra mussel invasion. The before period included 1973-1989 data from before the first sighting of zebra mussels in Lake Huron (Nalepa, 1995; U.S. Geological Survey, n.d.) and the after period included 1993-2016 after confirmed mussel establishment in Georgian Bay in 1993 to end of study (Wormington et al., 1995). Two RDAs were used to investigate drivers of the phytoplankton community investigating time periods of AOC designation and mussel invasion. Both the PERMANOVA and RDA were run using the vegan package (Oksanen et al., 2024).

Generalized Additive Mixed Models using the *mgcv* package (Wood, 2011) in R statistical software was used to identify significant time periods of change in total phytoplankton biovolume and within the 7 major phytoplankton divisions: Bacillariophyta, Chlorophyta, Chrysophyta, Cryptophyta, Cyanophyta, Dinophyta, and Euglenophyta. The models primarily utilized the tweedie family although one model utilized a poisson family. Models were built to investigate factors such as year, station, and explanatory water quality variables including TP, TNN, and WT. Variables such as TAN, N:P, TON, and TN did not improve models and thus was not included. After identifying the most suitable model, it was checked for the influence of autoregression and moving averages to improve the model's AIC (Akaike, 1998; Pearce et al., 2011). All statistical plots and visualizations were created using the *ggplot2* package in R (Wickham, 2016).

3.3 Results

3.3.1 Total biovolume

Overall levels of phytoplankton biovolume in Severn Sound have decreased since sampling began in 1973 (Figure 3.1). Station P1 in the Penetang Harbour had the largest level of phytoplankton when sampling began and although it saw a decrease in phytoplankton, it is still the station with the highest phytoplankton biovolume. Station BS generally had and still has the lowest phytoplankton biovolume when compared to other stations.

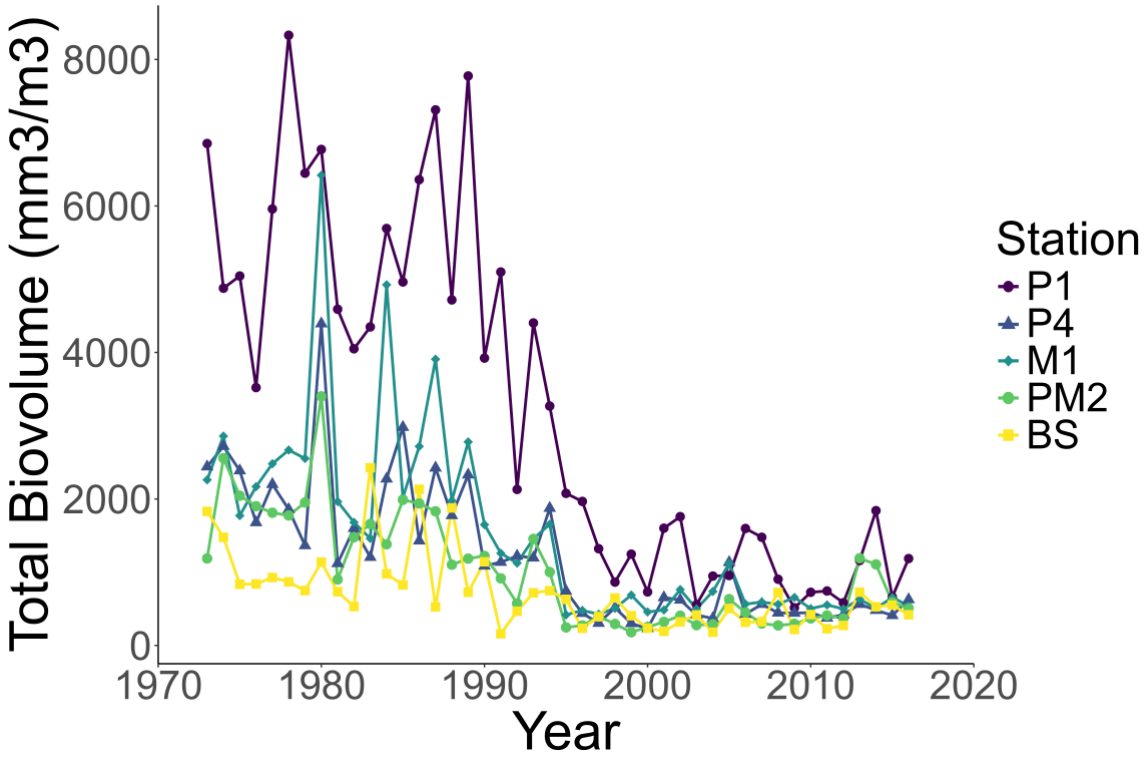

Figure 3.1. Trends in total biovolume (mm^3/m^3) of phytoplankton across long-term sampling sites in Severn Sound.

A GAMM was fitted to the total biovolume data using a tweedie family and REML estimation. When investigating changes in total biovolume, it was found that the

best model included year, station, and TNN which together explained 83% of the variance in biovolume ($R^2 = 0.83$) (Table 3.1, Figure 3.2, Table B1). TP was a significant term when included ($p<0.05$), however, the models' AIC was lower (<2 units) with TNN as a significant model term when compared to TP. Therefore, TNN was chosen as the better parameter to be included in the model. WT was tested as an explanatory variable; however, it did not improve the model and was not included. Temporal autocorrelation was modeled with the AR term set to p=1. When investigating how total biovolume changes, the GAMM illustrates a significant decrease in total biovolume from the late 1980s to the beginning of the 2000s.

Table 3.1. Best model for total phytoplankton biovolume and division phytoplankton biovolume (mm^3/m^3) Generalized Additive Mixed Models from 1973-2016. Final model included year, DOY, station, significant water quality explanatory variables, and autoregression and moving averages if they improved model AIC.

Parameter	Family	Final Model	R^2
Total Biovolume	Tweedie	TotalBiovolume ~ s(YEAR) + STATION + s(TNN), correlation = corARMA(form = ~1|YEAR, p=1)	0.825
Bacillariophyta	Tweedie	Bacillariophyta ~ s(YEAR) + STATION + s(TP) + s(TNN), correlation = corARMA(form = ~1|YEAR, p=1)	0.696
Chlorophyta	Tweedie	Chlorophyta ~ s(YEAR) + STATION + s(TP) + s(TNN)	0.604
Chrysophyta	Tweedie	Chrysophyta ~ s(YEAR) + STATION + s(TP) + s(TNN), correlation = corARMA(form = ~1|YEAR, p=1)	0.383
Cryptophyta	Tweedie	Cryptophyta ~ s(YEAR) + STATION + s(TP) + s(WT), correlation = corARMA(form = ~1|YEAR, p=1)	0.834
Cyanophyta	Tweedie	Cyanophyta ~ s(YEAR) + STATION + s(TP), correlation = corARMA(form = ~1|YEAR, p=1)	0.254
Dinophyta	Tweedie	Dinophyta ~ s(YEAR) + STATION + s(TP) + s(TNN)	0.722
Euglenophyta	Poisson	Euglenophyta ~ s(YEAR) + STATION + s(TP) + s(WT)	0.810

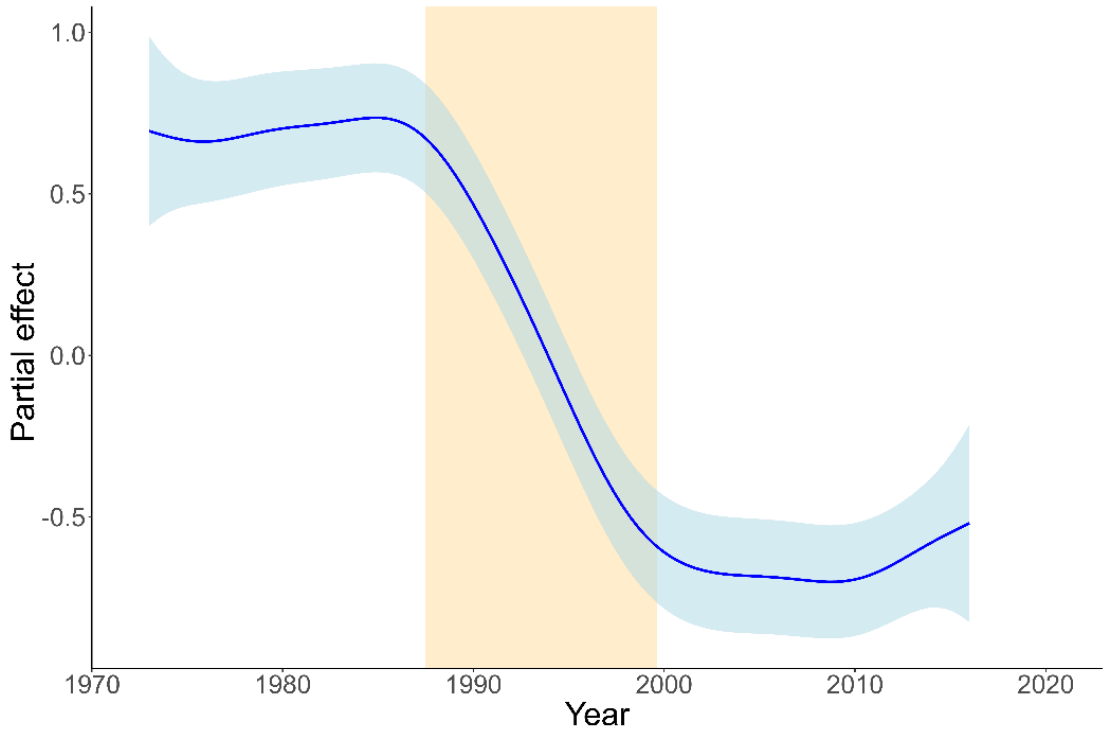

Figure 3.2. Partial effects plot of year on total biovolume (mm^3/m^3) Generalized Additive Mixed Model (GAMM) in Severn Sound from 1973-2016 with the blue ribbon indicating the 95% confidence interval, orange rectangles indicate areas of significant decrease and purple indicates areas of significant increase based on the first derivative of the model term.

3.3.2 Phytoplankton divisions

When investigating how phytoplankton taxonomic divisions have been impacted in Severn Sound, the five stations all have seen an overall decrease in phytoplankton abundance across the seven divisions (Figure 3.3). The five stations also experienced a shift in phytoplankton community composition across the sampling period (Figure 3.4). Some shifts are seen across the region such as an overall decrease in Bacillariophyta abundance. However, some shifts are station specific such as a large increase in the relative abundance of dinophytes at station BS.

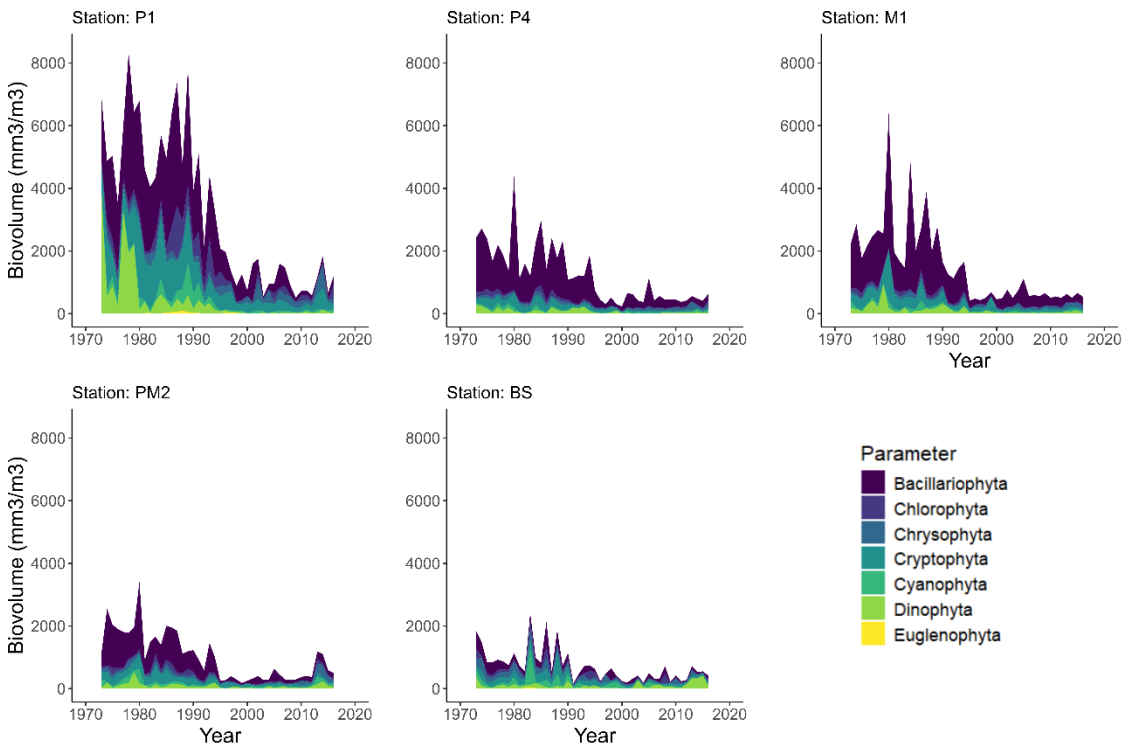

Figure 3.3. Biovolume (mm^3/m^3) of phytoplankton divisions across long-term sampling sites in Severn Sound from 1973-2016.

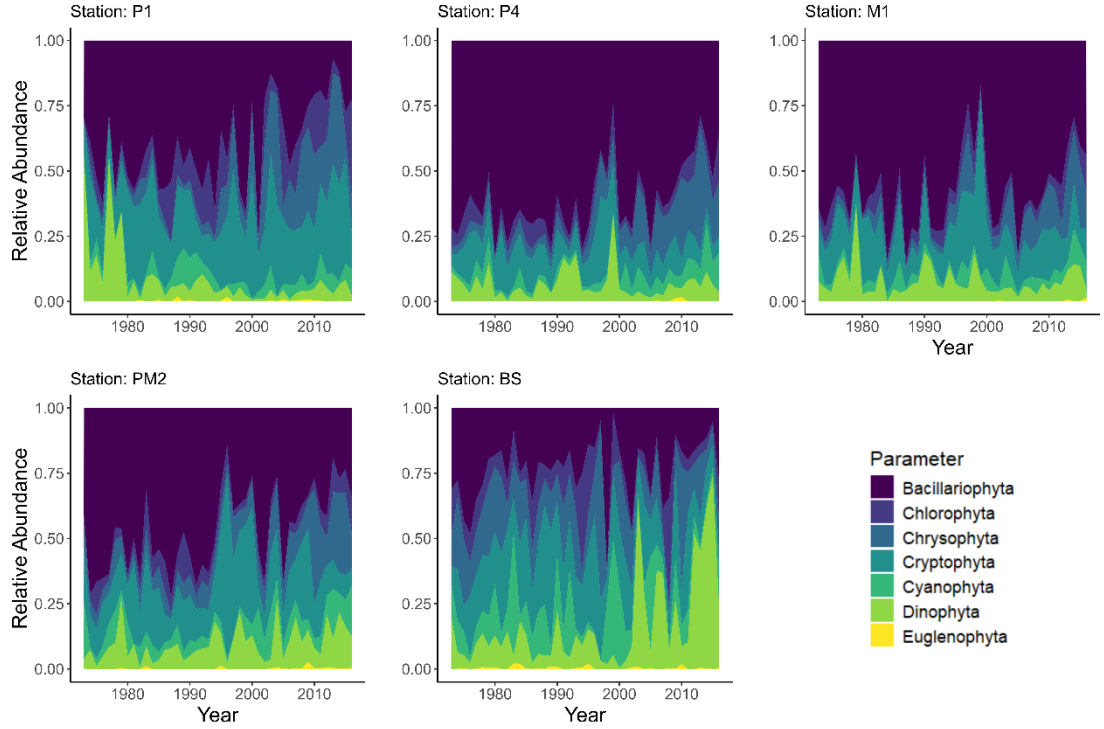

Figure 3.4. Relative abundance (%) of phytoplankton divisions across long-term sampling sites in Severn Sound from 1973-2016.

Two RDAs models were produced to assess changes during different AOC statuses (before, during, and post-AOC delisting) as well as changes before and after the zebra mussel invasion (Figure 3.5). Both RDAs had Chla, TP, and WT as significant variables, however, the RDA exploring zebra mussels also included TNN and TN as significant parameters. The RDA investigating AOC status explained 11.1% variation in cyanobacterial community composition in Severn Sound, where Axis 1 explained 7.8% variation and the second axis explained an additional 2.3% variation. It also showed overlap between the pre and during AOC listing periods, although during had more variation, and both of these periods separate from the post listing period. Before and during AOC listing periods correlated with higher Chla and TP, and lower WT, whereas the after AOC listing period correlated with lower Chla and TP, and higher WT. Phytoplankton community mostly clustered in the middle however, Bacillariophyta correlated more with the before and during AOC listing period, and Chrysophyta correlated more with the after AOC listing period. The RDA exploring impacts from the zebra mussel invasion explained 19.1% variation in cyanobacterial community composition in Severn Sound, where Axis 1 explained 11.7% variation and the second axis explained an additional 4.2% variation. It was similar to the AOC status RDA with high Chla and TP, and low WT correlating with the before invasion period and low Chla and TP, and high WT correlating with the after invasion period. TN and TNN did not correlate strongly with either period, however TNN was strong negatively correlated with TN, although TN had low explanatory strength in the RDA, and TNN was also moderately negatively correlated with TP.

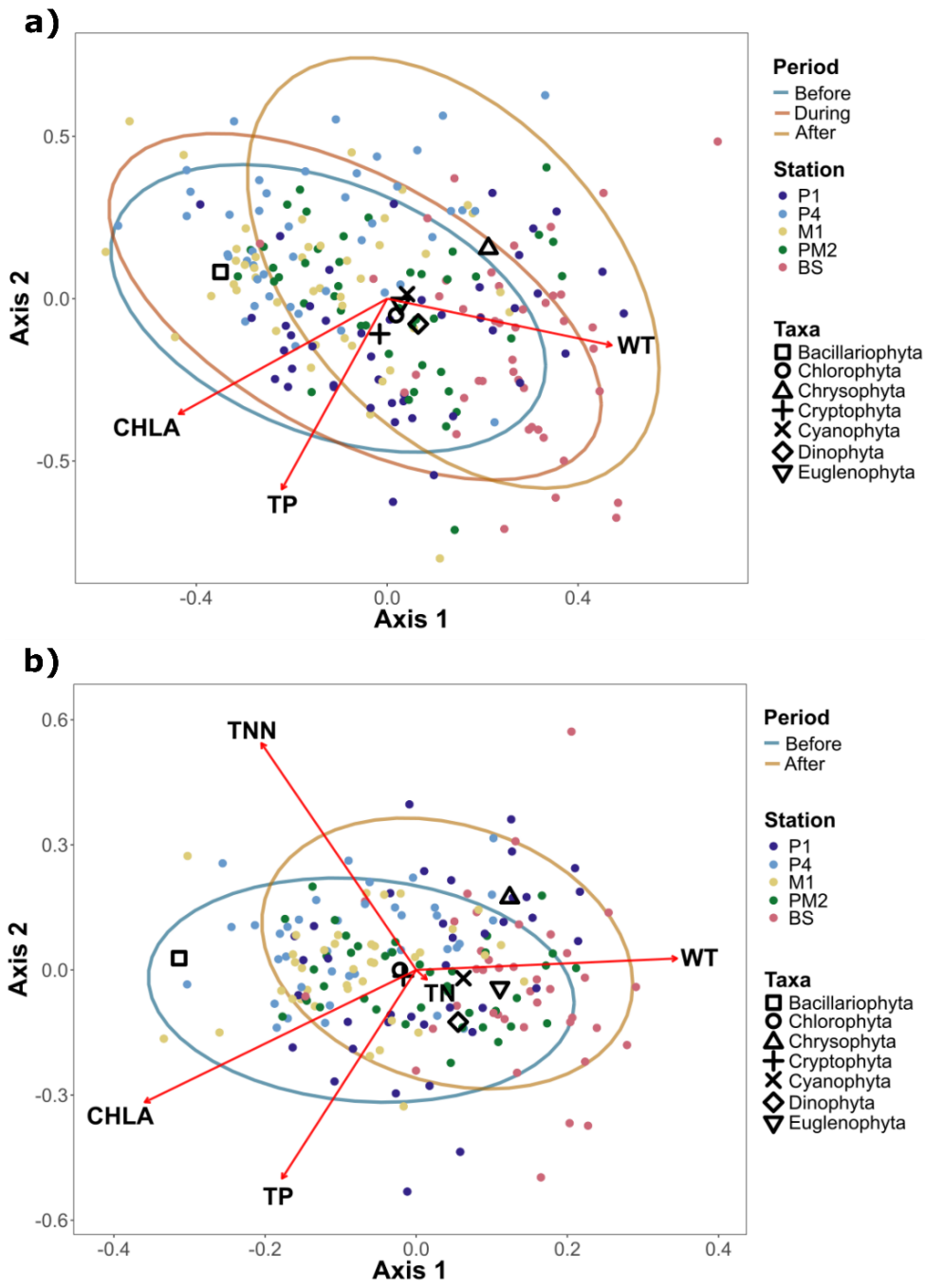

Figure 3.5. Redundancy Analysis (RDA) biplot of phytoplankton division biomass in Severn Sound a) before Area of Concern (AOC) designation (1973-1986), during AOC designation (1987-2002) and after delisting of AOC designation (2003-2016) and b) before the zebra mussel invasion (1973-1989) and after zebra mussel establishment (1994-2016). Only significant parameters (p-value <0.05) were included in the final model. TNN = total nitrate/nitrite, TN = total nitrogen, TP = total phosphorus, Chla = chlorophyll *a* (discontinued after 2008), WT = water temperature.

Two PERMANOVAs were conducted to detect significant differences in the phytoplankton communities during pre-AOC status, during AOC status, and post-AOC status as well as before and after the zebra mussel invasion. The PERMANOVA conducted on AOC status detected significant differences in the community across stations (p-value <0.05), as well as a significant difference in the periods (p-value <0.05) (Table 3.2). In addition, the PERMANOVA conducted on pre and post zebra mussel invasion also showed significant differences (p-value <0.05) in the phytoplankton community across stations and pre and post zebra mussel invasion (Table 3.3).

Table 3.2. Permutational Multivariate Analysis of Variance (PERMANOVA) of phytoplankton community in Severn Sound. Period includes before Area of Concern (AOC) status (1973-1986), during AOC designation (1987-2002) and after delisting of AOC status (2003-2016). Significant p-values are bolded (p-value <0.05).

Variance Index	Df	R^2	F-value	p-value
Station	4	0.214	18.35	**<0.001**
Period	2	0.085	14.52	**<0.001**
Station:Period	8	0.104	4.48	**<0.001**
Residual	205	0.597		

Table 3.3. Permutational Multivariate Analysis of Variance (PERMANOVA) comparing phytoplankton community in Severn Sound before the zebra mussel invasion (1973-1989) and after zebra mussel establishment (1994-2016). Significant p-values are bolded (p-value <0.05).

Variance Index	Df	R^2	F-value	p-value
Station	4	0.202	14.37	**<0.001**
Period	1	0.079	22.40	**<0.001**
Station:Period	4	0.068	4.82	**<0.001**
Residual	185	0.651		

GAMMs were fitted to each of the seven phytoplankton divisions (Table 3.1, Figure 3.6). Each division was tested with model terms year, station, water quality parameters (TP, TNN, and WT), and auto regression/moving average. All models improved with the inclusion of year and station, but different division improved with the inclusion of differing water quality parameters. TP was a significant model term for all divisions, but TNN and WT varied and generally did not overlap. Bacillariophyta's final model included model terms station, year, TP and TNN, and AR term p=1with an R^2 = 0.67 (Table B2). This division experienced a significant decrease during the late 1980's to the early 2000's. Bacillariophyta did not experience any increases in biovolume and thus levels of this division remained low after the 2000s and no recovery was experienced.

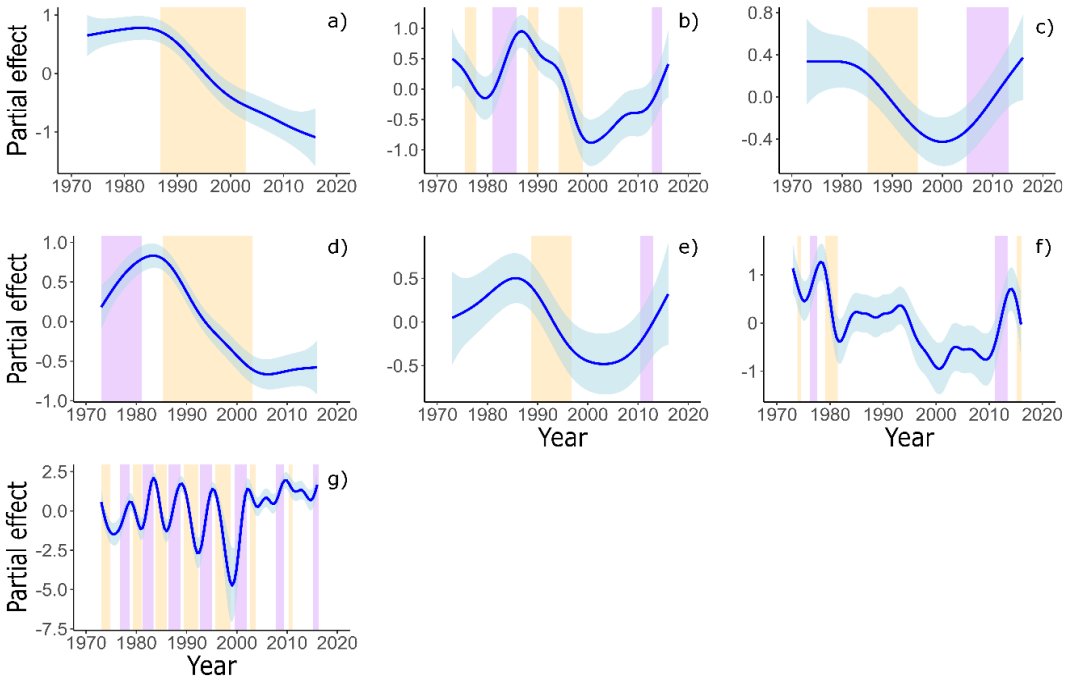

Figure 3.6. Partial effects plot of year on Bacillariophyta (a), Chlorophyta (b), Chrysophyta (c), Cryptophyta (d), Cyanophyta (e), Dinophyta (f), and Euglenophyta (g) biovolume (mm^3/m^3) Generalized Additive Mixed Model (GAMM) in Severn Sound from 1973-2016 with the blue ribbon indicating the 95% confidence interval, orange rectangles indicate areas of significant decrease and purple indicates areas of significant increase based on the first derivative of the model term.

The Cholorophyte final model included model terms station, year, TP and TNN with an $R^2 = 0.60$ (Table B3). Chlorophyta experienced a bit more variability in significant trends of biovolume than most of the other divisions. Before the 1990s, this division decreased in biovolume then experienced a longer increase throughout the 80's. During the 1990s Chlorophyta experienced two significant periods of declining biovolume. Following this decline this division increased throughout the 2000's and 2010's, however, only a small portion of this time frame was considered significant. The Chrysophyta final model included model terms station, year, TP and TNN, with p=1 and with an $R^2 = 0.38$ (Table B4). Chrysophyta experienced a significant decline from the mid 80s to the mid 90s then a significant increase in biovolume from the mid 2000's to the early to mid 2010's. The amount of biovolume decrease was relatively similar to the increase and thus overall, this division did experience a recovery in biovolume levels and there was no overall change in biovolume. The Cryptophyta final model included model terms station, year, TP and WT with an $R^2 = 0.83$ (Table B5). This division experienced a significant increase in biovolume during the 1970's. The cryptophytes experienced the longest decrease in biovolume spanning almost two decades from the mid 1980s to the mid 2000s. Due to this drastic decrease, cryptophyte levels were much lower by the 2010's compared to the 1970s.

The Cyanophyta final model included model terms station, year, TP, and $p = 1$ with an $R^2 = 0.25$ (Table B6). Cyanophyta experienced a non-significant increase from the 70's to mid 80's. This division then experienced a decline in biovolume throughout the 90s, similar to the majority of the other divisions, however, this division did start increasing throughout the 2000's and 2010's with a significant expansion period in the

early 2010s. Overall, Cyanophyta biovolume levels are most comparable at the beginning and end of the sampling timeframe. The Dinophyta final model included model terms station, year, TP and TNN with an $R^2 = 0.722$ (Table B7). Dinophyta experiences more variability in biovolume levels than most other divisions. Periods of increase and decrease tend to span a short period of time with some significant fluctuations in the mid 1970s to the mid 1980s and during the 2010s. From the 1980s to the 2010s, changes in biovolume are all non-significant and tend to vary, however, during the mid 1990s to the early 2000s there is a non-significant decrease in biovolume similar to the other divisions.

The euglenophyte division was not abundant across Severn Sound and thus the poisson family distribution was used to address the zero-inflated data. The final model included model terms station, year, TP and WT with an $R^2 = 0.81$ (Table B8). Euglenophyta experienced the most variability in changes to biovolume. Throughout the entire sampling period this division experienced short, but significant periods of increase and decrease in biovolume. This is likely due to the zero-inflated data as Euglenophyta is a rarer division in this region and thus was not always seen at stations throughout the sampling period. Overall Euglenophyta biovolume levels are similar at the start and end of the sampling period indicating that although this division experienced high variability, there was no overall change.

3.4 Discussion

3.4.1 Total biovolume

Total phytoplankton biovolume has decreased in Severn Sound during the 43-year (1973-2016) period investigated, specifically during the late 1980s and throughout the 1990s. This decrease has also been seen in other areas of Lake Huron, such as Saginaw Bay, and other Great Lakes such as Lake Erie and Lake Ontario (Bierman et al., 1984; Barbiero et al., 2006; Nicholls et al., 2002). My findings showed that TNN levels were more strongly associated with total phytoplankton biovolume over the 43 years studied, while both TP and TNN were significant predictors, model selection via AIC indicated that TNN alone provided the best model fit.

The RDA performed in this study showed a negative correlation between TP and TNN, and with both variables being significant in the GAMM as explanatory variables of phytoplankton biovolume this may suggest the phytoplankton community may be co-limited by TP and TNN at different times over the study period. Phytoplankton abundance is strongly associated with nutrient levels, specifically phosphorus and nitrogen which can be co-limiting (Peng et al., 2021). Phosphorus is a well-established limiting nutrient for phytoplankton growth in inland waters of the Great Lakes basin, particularly over longer time scales (Sterner, 2008). The GLWQA has led to decreases in phosphorus loadings since the 1970s which has caused a decrease in phytoplankton abundance in the Great Lakes. (Nicholls et al., 2002; Nicholls & Hopkins, 1993).

The decrease observed in the total biovolume GAMM began slightly before the introduction of zebra mussels, likely due to phosphorus reduction strategies aimed at limiting phytoplankton biovolume that were already underway in Severn Sound (Severn

Sound Remedial Action Plan, 1988). In addition to nutrient availability, it is likely that the zebra mussel invasion influenced total phytoplankton biovolume as zebra mussels are filter feeders that can eat large quantities of phytoplankton. Throughout the 1990s, during the early stages of the zebra mussel invasion, there was a drastic decrease in phytoplankton biovolume. In addition to direct influences from filter feeding, zebra mussels also impact phytoplankton abundance by altering nutrient availability and increasing water clarity (Fishman et al., 2010; Cha et al., 2011). Total phytoplankton biovolume has decreased across the Great Lakes, including Lake Huron, and have been tied to both nutrient load reductions and the introduction of zebra mussels (Barbiero et al., 2006; Nicholls & Carney, 2011; Fishman et al., 2010; Stefanoff et al., 2018 Winter et al., 2011).

In addition to temporal shifts, there have also been spatial changes to total biovolume. Although relatively close in proximity, the five long-term monitoring stations in Severn Sound show differences in total phytoplankton biovolume. Station was a significant variable in the total biovolume GAMM indicating although relatively close in proximity, the five long-term monitoring stations in Severn Sound differ in overall total biovolume. This study also found P1 to have higher total phytoplankton biovolume in the 1970s and 1980s. All stations experienced decreases biovolume, and in more recent years all stations have much less phytoplankton but P1 does still have higher levels than the other stations but not to the same degree as previously. At the beginning of AOC status designation, it was found that stations in Severn Sound had differing water quality profiles and phytoplankton biovolumes, with station P1 experiencing high nutrients and phytoplankton compared to other stations (Severn Sound Remedial Action Plan, 1988).

3.4.2 Phytoplankton divisions

The seven major phytoplankton divisions also saw changes throughout the study. All divisions had TP as a significant predictor, which is interesting considering that TNN was a stronger predictor for total biovolume. This is likely due to the substantial decrease in phosphorus (i.e., making it more of a growth limiting nutrient), as well as the inherent differences in the phosphorus and nitrogen requirements of different divisions that can impact models differently (Bai et al., 2022; Donald et al., 2013). Although the GAMMs explained a large portion of variance in Dinophyta and Euglenophyta biovolumes, both divisions exhibited a high degree of oscillation. This likely arises from the intermittent and low-abundance nature of these divisions, which leads to frequent fluctuations in observed biovolumes and consequently more pronounced ups and downs in the modelled trends over time, relative to higher abundance divisions where biovolume changes are smoother.

The Cyanophyta division had the lowest portion of variance explained by the model (R^2 = ~25%), compared to other divisions, which may reflect the highly opportunistic and seasonal growth dynamics of cyanobacteria. Cyanophytes exhibit rapid proliferation and senescence (Harris et al., 2024; Tarafdar et al, 2023; Wang et al., 2021), leading to abrupt fluctuations in biovolume that are challenging to capture using models based on composite seasonal mean samples. In this study samples were pooled across the May-September growing season, which may have muted short-term seasonal peaks and senescence events, further reducing the model's explanatory power. Additionally, the models only consider water quality variables and did not incorporate biotic interactions, such as grazing pressure or competition, which are known to strongly influence

cyanobacterial abundance and community dynamics (De Stasio et al., 2014; Polyak & Sukharevich, et al., 2025; Wang et al., 2010). These results highlight the need for further research that incorporates higher temporal resolution sampling and considers both environmental drivers and biotic interactions to better understand the mechanisms controlling cyanobacterial dynamics and their potential role in HABs (Chorus, 2001).

Many divisions in Severn Sound saw a decrease in the mid to late 80s when phosphorus reduction strategies were being introduced and align with decreases in total biovolume. During this time in Lake Simcoe, bacillariophytes decreased in Cook's Bay, a eutrophic portion of the lake, and cyanophytes and chlorophytes decreased across all basins related to lake wide phosphorus reduction and dreissenid mussels (Winter et al., 2011). Although many divisions saw decreases in abundance during the introduction of phosphorus mitigation strategies, many divisions also saw steep decreases in the early to mid 1990s, which may reflect impacts from the zebra mussel invasion. Zebra mussels preferentially consume phytoplankton that are weak swimmers or fall within their optimal prey size range, while species such as *Microcystis* are consumed at much lower rates (Lavrentyev et al., 1995). Phytoplankton that are strong swimmers, have faster growth rates, or otherwise avoid ingestion tend to be more resistant to predation and can maintain their populations despite mussel presence (Lavrentyev et al., 1995). In addition to direct effects from feeding, zebra mussels increase water clarity from high volumes of filter feeding that can promote light tolerant species with oligotrophic preferences (Fisherman et al., 2010). Changes in phytoplankton communities have been seen in the 2000s in Lake Huron, including an increased portion of phytoflagellates such as cryptophytes and

chrysophytes due to the introduction of zebra mussels and warming (Barbiero and Tuchman, 2001; Reavie et al., 2025).

Water temperature affects phytoplankton species differently due to species differences in temperature optima. Water temperature was found to be a significant driver of the Cryptophyta and Euglenophyta divisions in this study. Although their relationship with temperature is less studied, cryptophytes and euglenophytes have been reported to be affected by warming temperature (Camoying & Trimborn 2023; Armi et al., 2010). Warmer temperatures can shift competitive dynamics among species, often favouring smaller, fast-growing cyanobacteria over larger bacillariophytes (Carey et al., 2012; Peng et al., 2021). Although cyanophytes are well-known for high optimal growth temperature (Carey et al., 2012; Peng et al., 2021), this study found that temperature was not a significant predictor in the cyanophyte GAMM, which could be due to multiple factors such as the pooling of data which includes data from spring, summer, and fall, and influences from other factors such as nutrients influencing this division more.

Station was significant across all phytoplankton division GAMMs and both PERMANOVAs. The PERMANOVAs indicate station was significant and had a significant interaction between station and period indicating that stations had differing phytoplankton communities as well as their communities were affected differently by changes to AOC status and the zebra mussel invasion.

The sampling stations in Severn Sound exhibited differing phytoplankton community composition at onset of AOC status destination. These differences were largely associated with variation in site characteristics, including lake morphometry and watershed land use (Severn Sound Remedial Action Plan, 1988). Both morphometry and

land use are well known to impact water quality in addition to biotic communities such as phytoplankton (Kakouei et al., 2021; Wu et al., 2023). Morphometry may have exerted indirect effects by influencing light availability, mixing depths, and residence time further contributing to spatial variation in phytoplankton communities (Reynolds, 2006). The persistence of these patterns in the present study suggest that these site-specific influences remain ecologically relevant.

The decreases in phytoplankton abundance and different changes within the seven major phytoplankton divisions were evident in the phytoplankton community profiles. Both RDAs show Chla, TP, and WT as significant drivers. It has previously been shown that decreases in phosphorus and shifts in N:P ratio have caused changes in phytoplankton community composition (Nicholls et al., 2002; Nicholls & Hopkins, 1993). In addition, zebra mussels have been shown to directly and indirectly alter phytoplankton community composition (Cha et al., 2011; Nicholls & Carney, 2011). Increases in water temperature have also been a growing concern due to their influence on phytoplankton community composition (Filiz et al, 2020). Changes to water temperature can alter bloom timing, community structure, and nutrient cycling (Yu et al., 2018). Shifts in temperature have been seen to influence phytoplankton abundance and community composition across the Great Lakes, including in Lake Huron (Reavie et al., 2025, Warner & Lesht, 2015).

Interestingly TNN and TN were only significant in the RDA investigating the influence of the zebra mussel invasion. This could be due to zebra mussels' impact on nitrogen cycling in aquatic systems, such as increasing ammonium recycling and changing nitrogen availability (Arnott & Vanni, 1996; Marzocchi et al., 2021). Both

PERMANOVAs and RDAs show significant differences in the before and after communities, indicating that both eutrophication management strategies and the introduction of the zebra mussel impacted phytoplankton community composition. The RDA associated with the zebra mussel invasion explained a higher variance than the RDA comparing AOC status, 19.1% compared to 11.7%. This suggests that zebra mussel presence had a stronger and more consistent influence on the phytoplankton community in Severn Sound than nutrient management strategies. However, the weaker signal in the AOC model may reflect the staggered implementation of management strategies across the watershed, as well as potential delays in ecological response. Some improvements in water quality may not have translated immediately into community-level changes, potentially masking the full influence of remediation efforts within the AOC framework. Many areas throughout the Great Lakes have experienced changes in phytoplankton community composition in the last 50 years due to changes in nutrients, water temperature, and the introduction of invasive species, thus, it is no surprise that Severn Sound has also seen shifts in community composition as well (Fisherman et al., 2010; Winter et al., 2011; Reavie et al., 2025).

3.4.3 Patterns and implications

This study documented significant long-term shifts in the phytoplankton community of Severn Sound, including an overall decline in total biovolume and changes in dominant taxonomic groups. The time series data reveal that especially before AOC status, stations had differing total biovolume, total biovolume of divisions, and relative abundances of divisions. These changes persisted with time, such as differing relative abundances of divisions across stations. Other changes were universal such as total

biovolume decreasing across all stations, especially station P1, that had a much larger phytoplankton biovolume at the beginning, before the 1990s Station P1 had the highest TP and chlorophyll a levels (Severn Sound Remedial Action Plan, 1988). After the 2000s total phytoplankton biovolume at the 5 stations became more similar.

These changes appear to be driven by a combination of management driven nutrient reductions, invasive mussel filtration and broader climate driven shifts. While nutrient control efforts likely reduced overall productivity, the dreissenid mussel invasion further suppressed phytoplankton biomass and altered community composition. Warming trends may have influenced certain taxa and amplified existing changes. The patterns observed in Severn Sound are consistent with those documented in Great Lakes undergoing simultaneous nutrient reductions and dreissenid mussel colonization. Such systems commonly exhibit declines in phytoplankton biomass, shifts in phytoplankton community, and altered seasonal dynamics. These findings suggest that the trajectories seen in Severn Sound are part of a broader reginal trend of ecosystem restructuring.

These findings highlight the need for adaptive management frameworks that account for multiple, interacting drivers of change, including invasive species, climate change, and legacy nutrient conditions. Conventional approaches aiming for ecosystem recovery following nutrient reductions may need to be reconsidered, particularly in systems experiencing multiple stressors like climate change and dreissenid mussel invasion. Importantly, the persistent spatial differences observed across sampling stations underscore the value of spatially explicit monitoring. Such approaches can reveal localized responses that may be obscured in system-wide assessments and help managers better identify areas of resilience or vulnerability. Continued monitoring of phytoplankton

communities, both over time and across space, remains essential for understanding long-term trajectories and guiding effective, site-sensitive management strategies.

3.5 References

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Chapter 4. Long-term dynamics of cyanobacterial communities in Severn Sound before and after eutrophication mitigation reveals significant community shifts

4.1 Introduction

Harmful algal blooms can have serious consequences for freshwater ecosystems due to their impacts to human health, wildlife, ecosystem health, and aesthetics. Some cyanobacterial species can cause harmful blooms by producing cytotoxins, neurotoxins, and hepatotoxins, which pose a health risk when ingested or inhaled (Carmichael, 2001; Taylor et al., 2013; Olson et al., 2020). Although cyanobacteria are an important part of phytoplankton communities and the aquatic food web, they can have negative impacts on ecosystems and their services when they grow to bloom-levels. These impacts can include decreasing light availability to other phytoplankton species, macrophytes, and fish, as well as fueling anoxia that harms fish and invertebrates (Paerl & Otten, 2013). Documented increases in cyanobacterial blooms worldwide have prompted growing concerns about their potential harm to freshwater ecosystems and human health (Ho et al., 2019).

Point and non-point source nutrient loading is a major cause of eutrophication, with phosphorus and nitrogen being the key nutrients driving algal growth across an array of aquatic ecosystems (Schindler et al., 2008; Paerl, 2009). Following the 1978 GLWQA, phosphorus was the nutrient targeted for control as it was deemed the main limiting nutrient driving eutrophication in the Great Lakes (De Pinto et al., 1986). Phytoplankton communities responded to phosphorus reductions in both biomass decline and

corresponding shifts in community composition (De Pinto et al., 1986; Bierman & Dolan, 1981). However, increasing temperature from climate change has been associated with increasing algal blooms within the Great Lakes, and these algal blooms tend to be harmful cyanobacterial species (Dobiesz & Lester, 2009; Woolway et al., 2022; Paerl et al., 2011).

In addition to changes in nutrient dynamics, the introduction of invasive dreissenid mussels have impacted phytoplankton community composition. Introduction of *D. polymorpha* was first noted in the Great Lakes in the late 1980s and discovered in Lake Huron in the early 1990s (Cha et al., 2011). Reduced phytoplankton biovolume seen throughout the 1990s was connected to the highly efficient filter-feeding dreissenids (Nicholls et al., 2002). In Saginaw Bay, Lake Huron zebra mussels had a significant impact on the phytoplankton community composition via selective feeding and causing an increase in light tolerant species such as *Microcystis*, and species with oligotrophic preferences (Fisherman et al., 2010). In addition to direct impacts from feeding, zebra mussels also affect nutrient dynamics, which in turn can shape community composition (Cha et al., 2011; Fisherman et al., 2010).

Severn Sound is an approximately 130-km^2 water body in Georgian Bay, Lake Huron, Ontario that has experienced excessive algal growth since the 1960s (Severn Sound Remedial Action Plan, 1993). Severn Sound was one of 43 AOC listed in 1987 under the Canada-US GLWQA (International Joint Commission, 1989). Severn Sound was designated as an AOC due to BUIs including eutrophication (Severn Sound Remedial Action Plan, 1993). Phosphorus was a key nutrient causing eutrophication from agriculture, urban run-off, and sewage treatment facilities (Severn Sound Remedial

Action Plan, 1993). Reducing phosphorus to reduce algal abundance was a major delisting objective. In 2003, Severn Sound was delisted as an AOC due to reduced nutrient inputs and decreased phytoplankton biovolume (Severn Sound Remedial Action Plan, 1993; Severn Sound Remedial Action Plan, 1988; Sherman, 2002). Although overall phytoplankton biovolume and phosphorus was effectively reduced during the period of remedial action, there remains concerns pertaining to algal growth, especially since periodic algal blooms still occur across Severn Sound.

To improve our understanding of cyanobacterial community dynamics in Severn Sound, I analyzed the long-term water quality and phytoplankton data (1973-2016) collected across 5 distinct stations to assess (1) changes in cyanobacterial community dynamics and composition over time, and (2) elucidate if certain environmental conditions were associated with shifts in community structure. I focused on three main taxa that were found across all sampling sites representing bloom-forming species: *Dolichospermum* (previously identified as *Anabaena*), *Aphanizomenon*, and *Microcystis*. Two of these genera (*Dolichospermum* and *Aphanizomenon*) are diazotrophic (i.e., nitrogen fixers), and all have toxin-producing species (Huisman et al., 2005).

4.2 Methods

4.2.1 Sample collection

This study analyzed cyanobacterial community dynamics and composition as a function of environmental conditions before and after eutrophication mitigation in Severn Sound, Ontario. Data were from the same dataset used in Chapter 3 that included

matched samples for water quality and phytoplankton collected between 1973-2016. The five sampling sites presented in this chapter are the same as depicted in Chapter 2 and 3 and as presented in Figure 2.1. Environmental parameters including TAN, TNN, TON, TN, TP, Chla, Z_{sd}, and WT were also used in this analysis, and their collection information is provided in Chapter 2. Nitrogen:phosphorus (NP, calculation of total nitrogen divided by total phosphorus) was also investigated.

4.2.2 Statistical analysis

Statistical analyses were performed in the open-sourced software R version 4.4.0 (R Core Team, 2024). Due to data not following normal distribution with common transformations, I used the non-parametric PERMANOVA (999 permutations) to compare differences in the cyanobacterial community during different AOC designations: before AOC designation (1973-1986), during AOC designation (1987-2002) and after delisting of AOC status (2003-2016) and to investigated impacts of the zebra mussel invasion (1973-1989), before the first sighting of zebra mussels in Lake Huron (Nalepa, 1995; U.S. Geological Survey, n.d.) and after confirmed mussel establishment in Georgian Bay in 1993 to end of study (1993-2016) (Wormington et al., 1995). Two RDAs were used to investigate drivers of the cyanobacterial community investigating time periods of AOC designation and mussel invasion. A significant RDA (P-value <0.05) was created using only significant environmental variables (p-value <0.05) included, and only the top 10 most abundant cyanobacteria genera to reduce noise from rare taxa. Both the PERMANOVA and RDA were run using the vegan package (Oksanen et al., 2024). RDA plots utilized package *ggplot2* (Wickham, 2016). N:P ratio was not included in the analysis due to the inclusion of TN and TP and inherent collinearity.

Relative abundance graphs were used to visualize changes across the five sampling stations in the most dominant cyanobacterial taxa: *Aphanizomenon*, *Dolichospermum*, and *Microcystis* and "other" which included all other genera pooled calculated using all cyanobacterial abundance data. All other genera including *Aphanocapsa, Aphanothece, Cbroococcus, Coelomoron, Cuspidothrix, Geitlerinema, Gloeocapsa, Gloetrichia, Limnoraphis, Limnothrix, Merismopedia, Oscillatoria, Phormidium, Planktolyngbya, Planktothrix, Pseudoanabaena, Radiocystis, Rhabdoderma, Romeria, Snowella, Synechococcus, Synechocystis, Trichodesmim, unid. cyanophyte, Woronichinia* were grouped into "Other" due to rare abundance levels throughout the sampling stations and period. Plots were made using package *ggplot2* (Wickham, 2016). Summary statistics were calculated for each of the top three dominant taxa across the entire sampling period for each embayment including mean, standard deviation, maximum, and n (number of samples) to illustrate differences across sampling stations for each genus. I conducted an ISA (Indicator Species Analysis) using R package *indicspecies* to determine if a community change of the top three taxa occurred (De Cáceres, & Legendre, 2009). To identify a meaningful temporal break point in cyanobacterial community structure breakpoint analysis was conducted on total biovolume of the top three taxa with R package *strucchange* (Zeileis et al., 2002). This approach was used to statistically determine the point in time when a significant shift occurred in the community.

I constructed GAMs using the *mgcv* package in R (Wood, 2011). This analysis allowed me to identify times of significant change in the three most common cyanobacterial genera and their significant explanatory variables. All models were best

described using a tweedie distribution and backwards selection was utilized in which all potential explanatory parameters were initially included in the model, then only significant (p-value <0.05) and potentially impactful (p-value <0.1) parameters were included in the next model and rechecked for significance and improvement of the Akaike Information Criterion (AIC) (Akaike, 1998). Concurvity was also checked to ensure no problematic nonlinear relationships among the predictors.

4.3 Results

The PERMANOVA results confirm there was a significant difference in the before, during, and after delisting period that explained approximately 31.2% of variation (F = 50.00, p-value <0.001) (Table 4.1). There was also a significant difference in the cyanobacterial community among stations, however, this only explained approximately 3.3% of the variation (F = 2.60, p-value 0.002). The Period:Station interaction was not statistically significant (F = 0.70, p-value = 0.90), indicating that all stations had a similar shift in cyanobacterial community composition before, during, and after delisting. The second PERMANOVA indicates a significant difference in the cyanobacterial community before and after the zebra mussel invasion (F = 65.69, p-value <0.001) (Table 4.2). This PERMANOVA also found a significant difference among stations to a lesser extent of only 3.3% of the variation (F = 2.21, p-value 0.011), and no statistical significance of the Period:Station interaction (F = 0.39, p-value = 0.97).

Table 4.1. Permutational Multivariate Analysis of Variance (PERMANOVA) of the Severn Sound cyanobacterial community from 1973-2016. Period includes before Area of Concern (AOC) status (1973-1986), during AOC designation (1987-2002) and after delisting of AOC status (2003-2016). Significant p-values are bolded (p-value <0.05)

Variance Index	Df	R^2	F-value	p-value
Station	4	0.033	2.60	**0.002**
Period	2	0.312	50.00	**<0.001**
Station:Period	8	0.017	0.70	0.898
Residual	204	0.637		

Table 4.2. Permutational Multivariate Analysis of Variance (PERMANOVA) comparing cyanobacterial community in Severn Sound before the zebra mussel invasion (1973-1989) and after zebra mussel establishment (1994-2016). Significant p-values are bolded (p-value <0.05).

Variance Index	Df	R^2	F-value	p-value
Station	4	0.033	2.21	**0.011**
Period	1	0.248	65.69	**<0.001**
Station:Period	4	0.006	0.39	0.974
Residual	189	0.713		

The first RDA explored relationships between cyanobacterial taxa and major environmental variables before, during, and after delisting (Figure 4.1). This RDA model explained 15.2% variation in cyanobacterial community composition in Severn Sound, where Axis 1 explained 12.8% variation and the second axis explained an additional 1.1% variation (Figure 4.1). The second RDA explored relationships between cyanobacterial taxa and major environmental variables before and after the zebra mussel invasion and explained 16.7% variation in cyanobacterial community composition in Severn Sound. Axis 1 explained 14.2% variation and the second axis explained an additional 1.1% variation. Both RDAs included the top 10 genera including *Aphanizomenon*, *Aphanothece*, *Chroococcus*, *Dolichospermum*, *Microcystis*, *Oscillatoria*, *Planktolyngbya*,

Pseudanabaena, *Snowella*, and *Woronichinia*, and had TN, TNN, TP, Chla, and WT as significant predictors of community composition. In both cases the majority of the top 10 genera, with the exception of *Aphanizomenon*, *Dolichospermum*, and *Microcystis*, were clustered in the middle with limited correlation with any of the significant water quality predictors or with either period. Some clustering of stations can be seen, however, period seems to be a more defining characteristic of the cyanobacteria community. These two RDAs had similar but slightly different relationships between water quality variables and taxa. The RDA investigating AOC status found a very strong positive correlation on Chla and TN both with a moderately strong positive relationship with TP. Total phosphorus had a very strong positive relationship with *Aphanizomenon* and *Dolichospermum*. These variables had a negative relationship with TNN and WT as well as *Microcystis*.

Aphanizomenon and *Dolichospermum* had a strong relationship with the before and during period and *Microcystis* had a strong relationship with the during and after period. During AOC status had much more variability and encompassed both the before and after periods. The RDA investigating before and after the zebra mussel invasion found a strong positive relationship between TP and TN and both had a strong positive relationship with *Aphanizomenon* and *Dolichospermum* and these variables had a moderately strong relationship with Chla. The before period correlated with increased TP, TN, Chla, *Aphanizomenon*, and *Dolichospermum*. The after period was correlated with increased WT and TNN and *Microcystis*. These variables were all negatively correlated with variables that correlated with the before period.

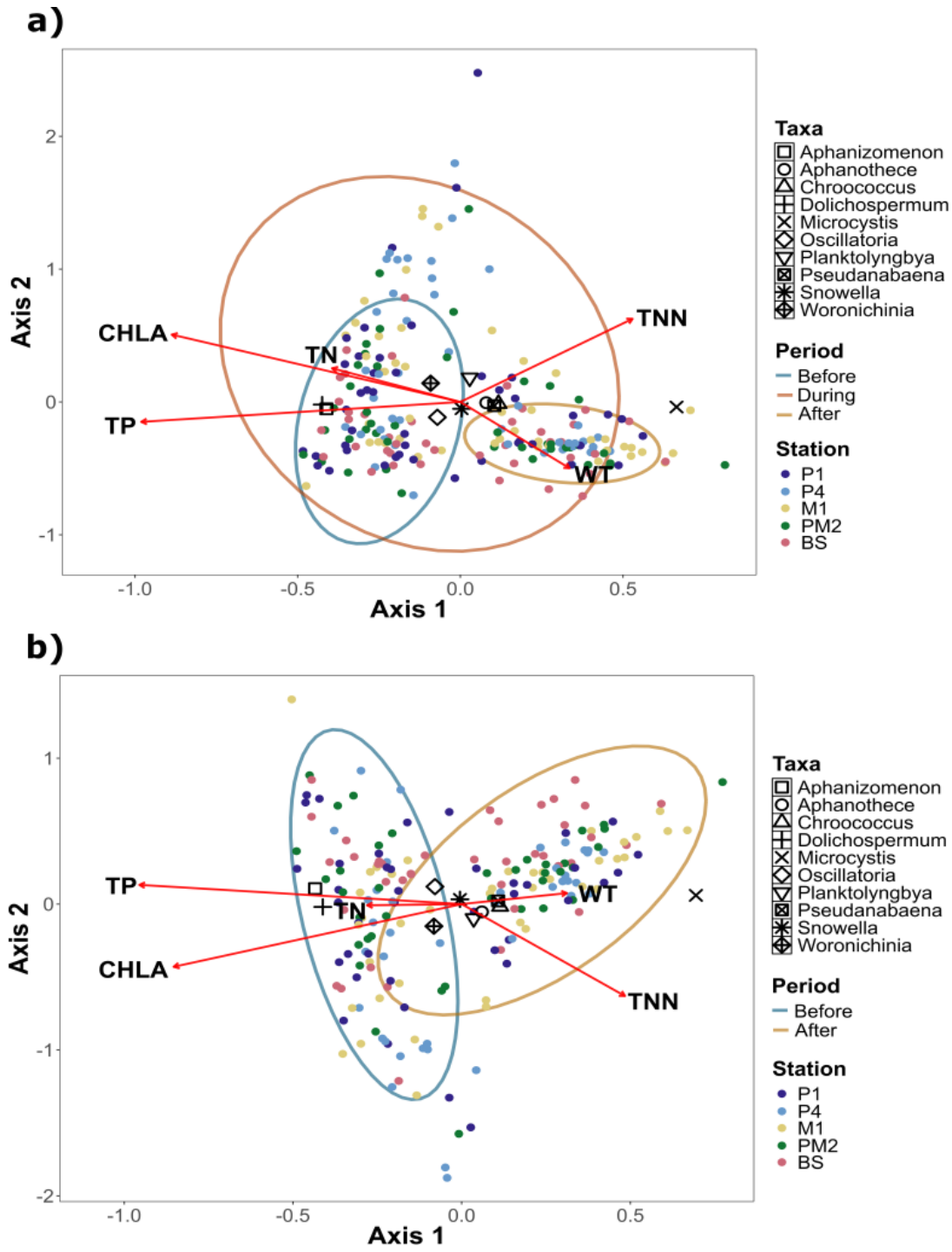

Figure 4.1. Redundancy Analysis (RDA) bioplot of cyanobacterial biomass in Severn Sound a) before Area of Concern (AOC) designation (1973-1986), during AOC designation (1987-2002) and after delisting of AOC designation (2003-2016) and b) before the zebra mussel invasion (1973-1989) and after zebra mussel establishment (1994-2016). The top 10 most abundant genera were included within the model. Only significant parameters (p-value <0.05) were included in the final model.

A relative abundance graph shows the most common genera found across the 5 sampling stations were *Aphanizomenon*, *Dolichospermum*, and *Microcystis* (Figure 4.2). Other genera were documented but were not as abundant across all 5 stations and during the sampling period. *Aphanizomenon* and *Dolichospermum* were more commonly seen at the stations prior to the 2000s, in which after, both genera decrease in relative abundance. This decrease in abundance is replaced by *Microcystis*, which becomes the most abundant genera in the 2000s for the rest of the sampling period. The other category includes all 25 other cyanobacterial genera found in Severn Sound, and overall relative abundance tends to differ between stations and from year to year.

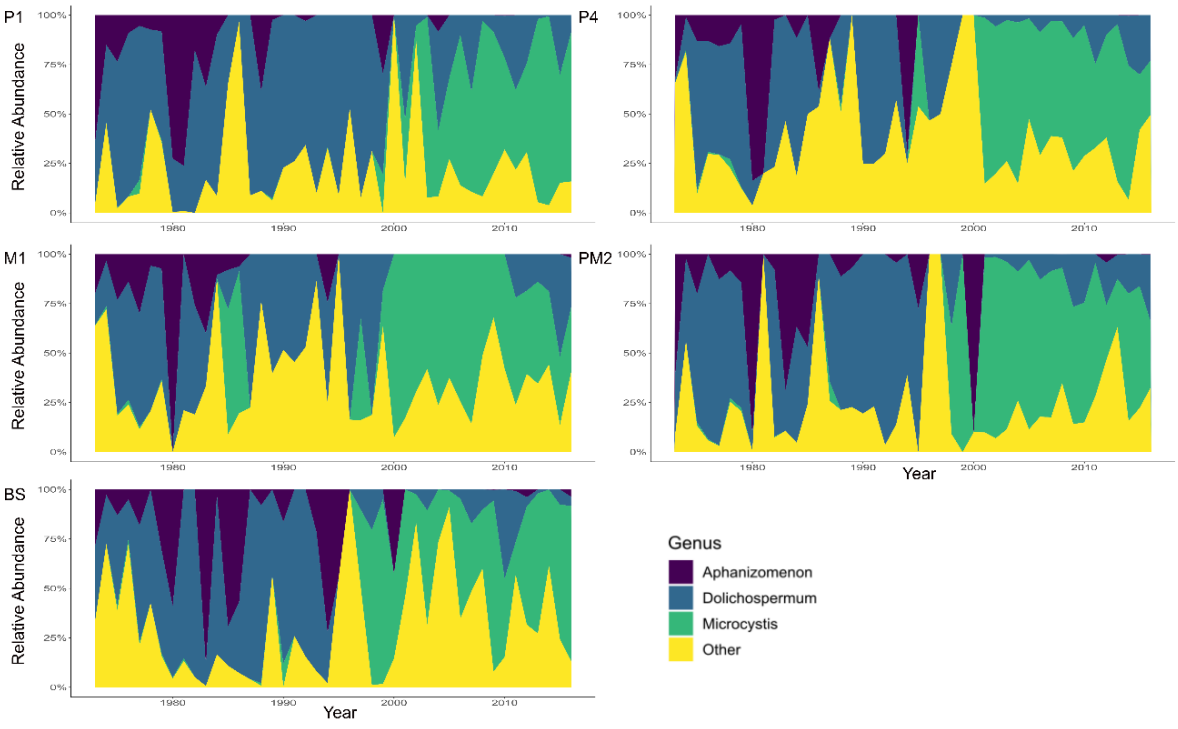

Figure 4.2. Relative abundance (%) of top three genera with other representing relative abundance of all other cyanobacteria genera found. Data is a pooled sample collected from the station during the collection period of that year from 1973-2016.

To investigate the three most abundant cyanobacterial genera at the five sampling stations in Severn Sound, summary statistics including mean, maximum, minimum, standard deviation, and n were compiled. The highest mean and maximum biovolume of *Aphanizomenon* during sampling was seen at station BS (Table 4.3). Whereas the lowest mean and maximum was seen at P4. *Dolichospermum* had the highest mean and maximum at P1, and the lowest mean and maximum at M1. M1 had the highest mean biovolume and maximum of *Microcystis*, and the lowest mean was found at P1, but the lowest maximum was at station PM2. In general, *Microcystis* and *Aphanizomenon* had lower mean biovolumes than *Dolichospermum*. Standard deviation was generally high, likely due to variation in biovolumes between years. Standard deviation was also higher at stations with higher maximum values, likely due to sporadic blooms increasing deviation.

Table 4.3. Summary statistics of the three most common cyanobacteria genera of five long-term sampling stations in Severn Sound from 1973-2016. Mean concentration of biovolume (mm^3/m^3), standard deviation (SD), maximum value, and number of samples (n)

Taxa	Station	P1	P4	M1	PM2	BS
Aphanizomenon	Mean	19.15	5.6	8.27	17.92	36.2
	SD	50.45	16.16	30.13	64.84	152.83
	Max	263	101	195	403	1007
	n	44	44	44	44	44
Dolichospermum	Mean	93.58	16.22	15.55	26.55	34.99
	SD	171.77	27.31	18.89	34.53	61.12
	Max	939	121	76	140	330
	n	44	44	44	44	44
Microcystis	Mean	12.2	8.73	13.29	10.86	12.98
	SD	22.46	14.73	35.64	16.43	31.6
	Max	89.65	63	233	54.69	169
	n	44	44	44	44	44

Indicator species analysis was used to determine if a significant change in cyanobacterial genera *Aphanizomenon*, *Dolichospermum*, and *Microcystis* occurred before and after 1990 as determined by the breakpoint analysis. *Dolichospermum* was not significantly associated with either period and thus was excluded from further indicator analysis results. *Aphanizomenon* was associated with before 1990 (IndVal = 0.855, p-value<0.05) and *Microcystis* was associated with after 1990 (IndVal = 0.781, p-value<0.05) (Table 4.4).

Table 4.4. Indicator Species Analysis (ISA) of cyanobacterial taxa pre- and post-1990. Indicator values (IndVal) represent the strength of association between individual taxa and time period. Only genera with statistically significant associations are shown. *Dolichospermum* did not show a significant association with either period and is excluded from the table. Significant p-values are bolded.

Taxon	Associated Period	IndVal	p-value
Aphanizomenon	Before 1990	0.781	**0.001**
Microcystis	After 1990	0.855	**0.001**

Generalized Additive Models were used to determine trends and explanatory variables for dominant cyanobacterial genera biovolume in Severn Sound. The final model for *Aphanizomenon* included Year, TP, TNN, and WT (R^2 adjusted = 0.38) (Table 4.4). The final model for *Dolichospermum* included Station, Year, and TN (R^2 adjusted = 0.442) (Table 4.5). The final model for *Microcystis* included Station, Year, TON, ZSD, and WT (R^2 adjusted = 0.226) (Table 4.6). *Aphanizomenon* experienced two periods of significant decrease, during the mid to late 1980s and during the 2000s (Figure 4.3). Although not statistically significant, an overall trend of decreasing biovolume can be seen from the mid 1980s to the late 2000s. *Dolichospermum* experienced a significant

decrease in biovolume during the 1990s and early 2000s, however, during the mid 2000s onwards, this genus has experienced a significant increase. When comparing significant trends in the three genera, *Microcystis* has the most variable trend. However, during the 1990s, this genus experienced a significant increase in biovolume that can also been seen when comparing the relative abundance of the three genera.

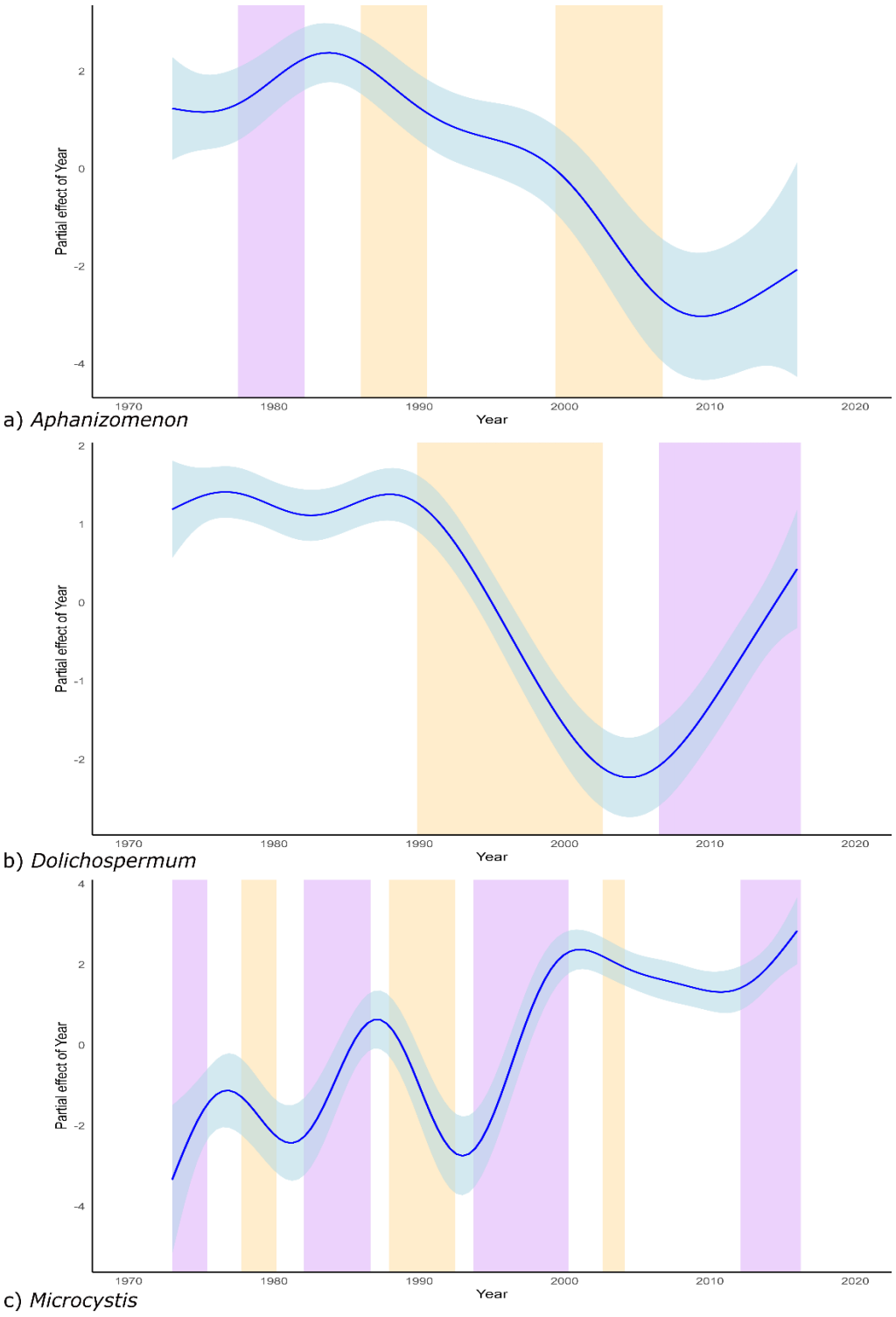

Figure 4.3. Partial effects plot of year of a) *Aphanizomenon*, b) *Dolichospermum*, and c) *Microcystis* biovolume (mm3/m3) GAMM in Severn Sound from 1973-2016 with the blue ribbon indicating the 95% confidence interval, orange rectangles indicate areas of significant decrease and purple indicates areas of significant increase based on the first derivative of the model term.

Table 4.5. Results of *Aphanizomenon* Biovolume (mm^3/m^3) Generalized Additive Model (GAM) from 1973-2016. Best model bolded. Significant p-values are bolded.

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth terms		
			estimate	Std. error	p-value	edf	F	p-value
Model 1	AIC = 943.27	Intercept	-0.50	0.69	0.47			
	adj R^2 = 0.666	StationP4	1.50	0.93	0.11			
	Family = tweedie	StationM1	0.77	0.82	0.35			
		StationPM2	1.05	0.87	0.23			
		StationBS	1.20	0.86	0.17			
		s(Year)				1.63	12.40	**<0.001**
		s(TP)				5.42	2.46	**0.022**
		s(TN)				3.14	1.85	0.120
		s(NP)				2.11	0.40	0.812
		s(TON)				1.00	4.90	**0.028**
		s(TNN)				1.00	7.02	**0.009**
		s(TAA)				1.84	1.87	0.141
		s(ZSD)				1.00	0.08	0.773
		s(WT)				1.00	8.96	**0.003**
Model 2	AIC = 944.79	s(Year)				6.19	8.94	**<0.001**
	adj R^2 = 0.374	s(TP)				5.48	2.40	**0.036**
	Family = tweedie	s(TON)				1.00	1.04	0.310
		s(TNN)				2.51	6.60	**<0.001**
		s(WT)				1.00	4.70	**0.031**
Model 3	AIC = 945.59	s(Year)				5.66	9.12	**<0.001**
	adj R^2 = 0.375	s(TP)				5.42	3.03	**0.009**
	Family = tweedie	s(TNN)				2.84	9.87	**<0.001**
		s(WT)				1.00	5.49	**0.020**

Table 4.6. Results of *Dolichospermum* Biovolume (mm^3/m^3) Generalized Additive Model (GAM) from 1973-2016. Best model bolded. Significant p-values are bolded.

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth terms		
			estimate	Std. error	p-value	edf	F	p-value
Model 1	AIC = 1719.02	Intercept	3.41	0.30	**<0.001**			
	adj R^2 = 0.615	StationP4	-1.11	0.50	**0.027**			
	Family = tweedie	StationM1	-1.20	0.38	**0.002**			
		StationPM2	-0.68	0.39	0.084			
		StationBS	-0.95	0.40	**0.017**			
		s(Year)				6.343	14.956	**<0.001**
		s(TP)				2.464	1.332	0.220
		s(TN)				1	4.215	**0.041**
		s(NP)				2.809	1.558	0.222
		s(TON)				1.004	2.6	0.108
		s(TNN)				1	4.913	**0.028**
		s(TAN)				1	2.96	0.087
		s(ZSD)				3.525	2.161	0.069
		s(WT)				1.866	0.331	0.848
Model 2	AIC = 1723.34	Intercept	3.36	0.27	**<0.001**			
	adj R^2 = 0.557	StationP4	-1.04	0.47	**0.026**			
	Family = tweedie	StationM1	-1.06	0.37	**0.004**			
		StationPM2	-0.55	0.37	0.139			
		StationBS	-0.75	0.32	**0.020**			
		s(Year)				6.181	17.937	**<0.001**
		s(TN)				1.841	4.667	**0.008**
		s(TNN)				1	9.03	**0.003**
		s(TAN)				1	0.268	0.605
		s(ZSD)				2.939	1.644	0.173
Model 3	AIC = 1723.98	Intercept	3.22	0.25	**<0.001**			
	adj R^2 = 0.442	StationP4	-0.90	0.35	**0.011**			
	Family = tweedie	StationM1	-0.98	0.33	**0.003**			
		StationPM2	-0.41	0.36	0.251			
		StationBS	-0.40	0.29	0.167			
		s(Year)				6.46	31.395	**<0.001**
		s(TN)				3.91	2.753	**0.024**

Table 4.7. Results of *Microcystis* Biovolume (mm^3/m^3) Generalized Additive Model (GAM) from 1973-2016. Best model bolded. Significant p-values are bolded.

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth terms		
			estimate	Std. error	p-value	edf	F	p-value
Model 1	AIC = 1166.26	Intercept	0.79	0.44	0.073			
	adj R^2 = 0.265	StationP4	0.03	0.72	0.970			
	Family = tweedie	StationM1	0.31	0.51	0.547			
		StationPM2	0.33	0.56	0.554			
		StationBS	0.47	0.67	0.488			
		s(Year)				8.49	12.34	**<0.001**
		s(TP)				2.84	0.37	0.788
		s(TN)				1.00	0.00	0.978
		s(NP)				3.65	0.81	0.457
		s(TON)				5.68	3.80	**<0.001**
		s(NN)				1	0.011	0.918
		s(AA)				1.00	0.00	0.955
		s(ZSD)				5.13	3.46	**0.003**
		s(WT)				5.10	3.02	**0.007**
Model 2	AIC = 1159.08	Intercept	1.03	0.29	**<0.001**			
	adj R^2 = 0.226	StationP4	-0.12	0.60	0.838			
	Family = tweedie	StationM1	0.03	0.39	0.929			
		StationPM2	0.06	0.34	0.869			
		StationBS	0.19	0.35	0.585			
		s(Year)				8.50	16.78	**<0.001**
		s(TON)				5.69	4.69	**<0.001**
		s(ZSD)				5.90	4.78	**<0.001**
		s(WT)				5.30	3.10	**0.005**

4.4 Discussion

The long-term collection of cyanobacterial data in Severn Sound presented a novel opportunity to not only investigate decadal community dynamics as a function of environmental conditions, including climate-driven temperature change, but also the ability to assess community shifts as a function of pre- and post-AOC listing. Overall, I found a major shift in the community from nitrogen-fixing genera *Aphanizomenon* and *Dolichospermum* to non-nitrogen fixing genera *Microcystis*. This was driven by changes in nutrients and temperature, with each genus being impacted by different environmental

factors. In addition, spatial differences in community composition were detected among stations, although these effects were weaker than temporal patterns. All three taxa have toxigenic species, so unfortunately there does not appear to be a community shift from toxin-producing to non-toxin producing taxa.

The cyanobacterial community in Severn Sound had clear changes in structure before and after the water body was delisted as an AOC. The community composition before delisting was associated with increased TP, TN, and Chla whereas the composition after was associated with increased TNN and WT. Regardless of listing period, nutrients such as TNN, TN, and TP were important drivers of cyanobacterial biomass and dominant taxa, especially *Aphanizomenon*, *Dolichospermum*, and *Microcystis*. Similar findings have been seen across the Great Lakes, where shifts in phytoplankton and cyanobacterial communities have been linked to shifts in nutrient profiles such as decreased phosphorus from GLWQA mandated mitigation efforts (Bierman & Dolan, 1981; Dobiesz & Lester, 2009; Fisherman et al., 2010; Nicholls et al., 2002).

Only minor differences in cyanobacterial community composition were found across the five sampling stations. This indicates that cyanobacterial communities are generally homogeneous across Severn Sound, even though previously there have been documented differences at different embayment sites of Severn Sound with notable differences in phytoplankton biovolume attributed to differing site characteristics such as morphometry, water mixing, and nutrient inputs (Severn Sound Remedial Action Plan, 1988). Even so, station was a significant factor in the PERMANOVA but accounted for only a small proportion of the variation (3%). Station was also a significant explanatory variable for both the *Dolichospermum* and *Microcystis* GAMs, but it was not a significant

explanatory variable for *Aphanizomenon*. *Aphanizomenon* had similar relative abundance levels across stations, whereas *Dolichospermum* and *Microcystis* had more variable abundance across stations. Overall trends in the cyanobacterial community composition were similar across stations, shown by the non-significant interaction between period and station.

Aphanizomenon was the only taxon to have TP as a significant explanatory variable. *Aphanizomenon* has decreased in other areas of Lake Huron, associated with decreased phosphorus levels (Bierman & Dolan, 1981). Total phosphorus has decreased across the Great Lakes and in other regions in Lake Huron and has been tied to GLWQA legislation requiring reduction in phosphorus inputs (Dolan & Chapra, 2012; Stadig et al., 2010). As an AOC, Severn Sound had specific goals to decrease phosphorus levels to reduce eutrophication, and meeting these goals supported delisting (Severn Sound Remedial Action Plan, 1988). *Dolichospermum* was strongly correlated with the before period within the RDA and although not significant in the GAM model, *Dolichospermum* was moderately associated with increased phosphorus. This taxon has been shown to be significantly reliant on phosphorus, with nitrogen acting as a secondary role in regulating its growth (Wan et al., 2019; Wang et al., 2018).

This study found that *Microcystis* was negatively correlated with TP, but did not have TP as a significant model term in the GAM. *Microcystis* is generally known for dominating with increased nutrients, specifically phosphorus (Orihel et al., 2012; Yang et al., 2022), however, *Microcystis* also has been shown to be resistant to low phosphorus conditions as it is an effective competitor for low phosphorus supply (Wan et al., 2019).

This may indicate, in part, why decreasing TP in Severn Sound may have contributed to the shift to a *Microcystis* dominated cyanobacterial community.

Although TP is a well-known driver of eutrophication, the role of different nitrogen forms on phytoplankton community composition and bloom dynamics can also be important. To assess the impacts of nitrogen speciation, various nitrogen forms, specifically TAN, TNN, TON, TN, and N:P, were tested to determine different potential nitrogen influences. Each of the three dominant genera had a different nitrogen form serving as an explanatory variable. Generalized Additive Models of *Aphanizomenon* included TNN, *Dolichospermum* included TN, and *Microcystis* included TON. *Dolichospermum* had TN as a significant explanatory variable and positively correlated with increasing TN, which has been seen in other studies due to increased energy costs from nitrogen-fixation (Wang et al., 2018; Celikkol et al., 2021). I found *Microcystis* increased with less TN and higher TNN and had TON as a significant model term, which shows a complex relationship between this taxon and nitrogen form.

Previous studies have documented shifts in cyanobacterial community composition as a function of different nitrogen forms (Monchamp et al., 2014). Some finds of this study align with previous research, such as TNN being a key driver of *Microcystis* abundance. However, other relationships differed, such as I observed a positive association between TN and *Aphanizomenon* and *Dolichospermum*, whereas Monchamp et al. (2014) reported negative relationships between TN and *Anabaena planktonica* and *Aphanizomenon flos-aquae*. This difference may reflect variations in nitrogen dynamics, as TN encompasses multiple chemical forms with varying bioavailability. Consequently, TN may capture a broader of nitrogen sources usable by

Aphanizomenon and *Dolichospermum*, which can exploit both inorganic and organic nitrogen, whereas *Microcystis* tends to rely more heavily on dissolved inorganic forms of nitrogen (Chen et al., 2019; Kramer et al., 2022; Pham et al., 2023). Differences may also stem from taxonomic resolution of analysis, as Monchamp et al. (2014) focused on specific species, whereas this study examined responses at a genus level.

In addition to nutrients, climate was also found to be an important driver of cyanobacterial community composition in Severn Sound. Water temperature was a significant explanatory variable in *Aphanizomenon* and *Microcystis* GAMs, and increased WT correlated with increased *Microcystis* and decreased *Aphanizomenon* and *Dolichospermum*. Increased WT was associated with the after delisting period and had a strong correlation with *Microcystis* in the RDA. This indicates that water temperature is higher after delisting than before, and that this increase in temperature is potentially negatively impacting *Aphanizomenon* and *Dolichospermum* and favouring *Microcystis*. Both *Aphanizomenon* and *Dolichospermum* have been shown to be less tolerant to increasing temperatures than *Microcystis*, with no difference between *Dolichospermum* and *Aphanizomenon* (Zhang et al., 2015), whereas *Microcystis* is known for having a higher optimal growth temperature as well as being more tolerant of increasing temperatures (Paerl & Huisman, 2008).

Microcystis has been increasing across the Great Lakes in recent years and increasing water temperature being associated with increased bloom events (Gobler et al., 2024; Woolway et al., 2022). Some research suggests that increasing temperatures could be driving increased algal blooms (Dobiesz & Lester, 2009; Paerl & Huisman, 2009) and impacting cyanobacteria community composition (Betros-Fortis et al., 2016), whereas

other research suggests temperature is a weaker driver of cyanobacteria blooms (Bonilla et al., 2023; Shchapov et al., 2025). In Severn Sound, water temperature was identified as a driver in the cyanobacterial community composition, however, the influence of WT on cyanobacterial dynamics appears to be taxon-specific, particularly *Microcystis* and *Aphanizomenon*. Increased WT shifting the cyanobacterial community in Severn Sound is a significant management concern as temperature in the Great Lakes is expected to continue to rise as a result of climate change (Xue et al., 2022).

Zebra mussels were first identified in the Great Lakes in the late 1980s and spread to Lake Huron by 1991 where they were confirmed in Severn Sound by 1993 (Nalepa & Gauvin, 1988; Nalepa et al., 1995; U.S. Geological Survey, n.d.). Zebra mussels have been shown to decrease phytoplankton abundance as well as shift the phytoplankton community composition in the Great Lakes with a notable effect on cyanobacterial communities as well (Bierman et al., 2005; Dobiesz & Lester, 2009; Fishman et al., 2010). Cyanobacterial community shifts in the 1990s have been associated with the introduction of zebra mussels in the Great Lakes including Lake Huron (Bierman et al., 2005; Dobiesz & Lester, 2009). This study identified 1990 as a significant break point in cyanobacterial community composition, with ISA showing a shift from *Aphanizomenon* dominance before 1990 to *Microcystis* dominance afterward. This temporal shift may reflect ecological changes associated with the zebra mussel invasion, that occurred around the same period.

In addition to impacts from direct feeding, zebra mussels have also been shown to impact nutrient cycles and control phosphorus availability leading to an increase in non-nitrogen fixing phytoplankton (Bierman & Dolan, 1981). This impact has also been seen

across North America and in other areas of Lake Huron such as Saginaw Bay, where the introduction of zebra mussels caused shifts in the cyanobacterial community due to impacts from selective feeding, increased water clarity, and disruption to nutrient dynamics (Cha et al., 2011; Bierman et al., 2005; Fisherman 2010; Vanderploeg et al., 2001). The RDA comparing before and after zebra mussel invasion explained a slightly higher variation in the cyanobacterial community than the RDA comparing AOC status. The RDA also found decreased Chla is associated with the after zebra mussel invasion period, and although TP and Chla are moderately positively correlated with each other, they are not strongly correlated, suggesting other factors are involved such as dreissenid mussels.

Secchi disk visibility was only a significant model term for *Microcystis,* which may indicate an association with increased water clarity and light due to zebra filter-feeding (Fisherman et al., 2010). *Microcystis* is commonly found to negatively correlate with Z_{SD} (Yu et al., 2014), likely due in part to *Microcystis* cell densities directly affecting Z_{SD} especially during bloom events. Likely Z_{SD} in this study illustrates the introduction of the invasive zebra mussels that consume large quantities of phytoplankton and increase water clarity (Fahnenstiel et al., 1995). Additionally, zebra mussels have also been shown to selectively feed on phytoplankton where they reject some toxic cyanobacteria species such as *Microcystis* in favour of non-toxic algae (Bierman et al., 2005).

With eutrophication being a major concern across the Severn Sound region since the 1960s, focused mitigation efforts driven by legislation (GLWQA) resulted in significant nutrient reductions from the late 1980s until present day. My analysis of the long-term dataset has shown that the cyanobacterial community over forty-seven years

has not only changed in response to climate (WT) and possibly zebra mussel introduction, but long-term shifts in community composition and biomass are associated with pre- and post-AOC listing periods. In summary, bloom-forming taxa *Aphanizomenon*, *Dolichospermum*, and *Microcystis* were found to be the most dominant genera in Severn Sound. *Dolichospermum* dominated the community pre-2000s, with *Microcystis* becoming dominant after this time. Total phosphorus, water temperature, nitrogen forms, specifically TN, TNN, and TON, and Secchi disk visibility were important drivers of changes in the cyanobacterial community composition.

Overall, the findings of this study emphasize the continued need for spatially resolved monitoring and nutrient management within Severn Sound and similar Great Lakes embayments. Although phosphorus control programs have substantially improved water quality, the observed variability in cyanobacterial community composition highlights the potential for nutrient imbalances that could sustain or shift bloom composition under changing environmental conditions. Continued vigilance is warranted as even modest increases in temperature or alteration in nutrient availability may promote the dominance of bloom-forming cyanobacteria. Future management should therefore consider how both phosphorus and nitrogen inputs and climate change may influence bloom risk. Sustaining long-term monitoring programs and adopting adaptive management approaches will be essential to maintain the ecological recovery achieved through past remediation efforts and to prevent the re-emergence of HAB related impairments in Severn Sound.

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Chapter 5. Nearshore water quality in Severn Sound is spatially variable and dissimilar to offshore water quality profiles.

5.1 Introduction

The nearshore zone is ecologically important because it represents a transitional habitat encompassing the shoreline and littoral zone that supports relatively high biological productivity and diversity in the lake environment (Vadeboncoeur et al. 2011). The nearshore is also the first area in a lake to receive tributary and runoff inputs from the watershed, which can be highly dynamic due to climate and land use factors. Even with this in mind, lake monitoring programs tend to occur in offshore (pelagic) areas approximating the "middle" of the open-water or, more typically, the deepest part of a lake to capture in-lake conditions (Burns et al., 1999). Although there are benefits to this approach, it misses the conditions of the lake where ~90% of biological activity can be occurring (Vadeboncoeur et al. 2011).

Nearshore and embayment regions of lakes often exhibit complex spatial variability in water quality due to morphometric differences such as depth, substrate, temperature, biogeochemical processing, and external drivers such as watershed influence (Vadeboncoeur et al. 2011). Investigations into the nearshore-offshore waters in the Great Lakes have demonstrated that nearshore regions tend to have greater nutrients than offshore regions and is often more variable and influenced by watershed inputs compared to more stable and isolated offshore waters (Yurista et al., 2016). Understanding how water chemistry varies between nearshore and offshore regions can provide important spatially explicit information for lake management, such as pollution hotspots.

Although there have been investigations of nearshore water quality across the Great Lakes, they have excluded certain areas, including Severn Sound (Howell et al. 2012, Howell et al. 2014, Howell and Holeton, 2023). Severn Sound is a large embayment-system in the eastern basin of Lake Huron. This waterbody is a delisted AOC), which is a designation granted by the binational Great Lakes Water Quality Agreement. Severn Sound was originally listed as an AOC in 1987 due to high nutrient concentrations and issues associated with eutrophication. By 2003, Severn Sound was delisted due to marked decreases in phosphorus and chlorophyll *a* (Sherman, 2002).

Meeting the criteria for listing and delisting was mainly informed by a long-term water quality monitoring program that started in 1973 by the Ontario Ministry of Environment. By the mid-1990s, this monitoring program was taken over by the Severn Sound Environmental Association. The Severn Sound water monitoring program followed conventional design criteria, including locating sampling sites that approximated the mid-point or deepest point of each embayment site. Although this sampling approach has produced valuable data documenting the distinct water quality profiles of each embayment in Severn Sound, there remains data and knowledge gaps surrounding the role of watershed inputs and nearshore conditions on the overall water quality picture in Severn Sound.

This study represents the first spatially comprehensive nearshore water quality assessment of Severn Sound. My objectives for this work were to (1) document a baseline of water quality conditions in the nearshore zone of Severn Sound; (2) assess water quality metrics as a function of embayment location; and (3) compare nearshore and offshore water quality profiles. I coordinated my sampling timeframe to occur

concurrently with the SSEA offshore monitoring program during the summer of 2022 (June-September). These results will help address knowledge gaps regarding nearshore water quality condition in Severn Sound and could be used to inform future management initiatives.

5.2 Methods

5.2.1 Study region and sampling sites

Severn Sound is a 130-km^2 embayment system in Georgian Bay, Lake Huron (Figure 5.1) that is largely separated from Georgian Bay. Nearshore and offshore sampling locations were located in the four main bays of Severn Sound: Penetang Harbour, Midland Bay, Hogg Bay, and Sturgeon Bay. The embayments in Severn Sound have multiple unique physiographic regions, differences in land use, and differences in lake morphometry that impact water quality (Severn Sound Remedial Action Plan, 1988). Four nearshore-sample sites were chosen per embayment, for a total of 16 sites. Though I aimed to widely distribute sites within each basin, ultimately site access dictated site location due to the high degree of privately owned shoreline. In total, there were 16 nearshore sites and 11 offshore sites from the SSEA monitoring program sampled in this study.

Each sampling site label consists of a three-part code: A prefix indicating nearshore (N) or offshore (O) station, an embayment code based on pre-established management labels: P for Penetang Harbour, M for Midland Bay, PM for Port McNicholl (located in Hogg Bay), and BS for Sturgeon Bay, followed by a site number. Offshore

sites were pre-designated by SSEA and retain their original label for consistency and traceability. In most cases these follow a standard numerical format, but in some cases reflect local naming conventions (Figure 5.1). Samples were collected once a month from June – September 2022. Nearshore samples were collected and processed at Ontario Tech University and offshore samples were collected and processed by the SSEA as described in Chapter 2.

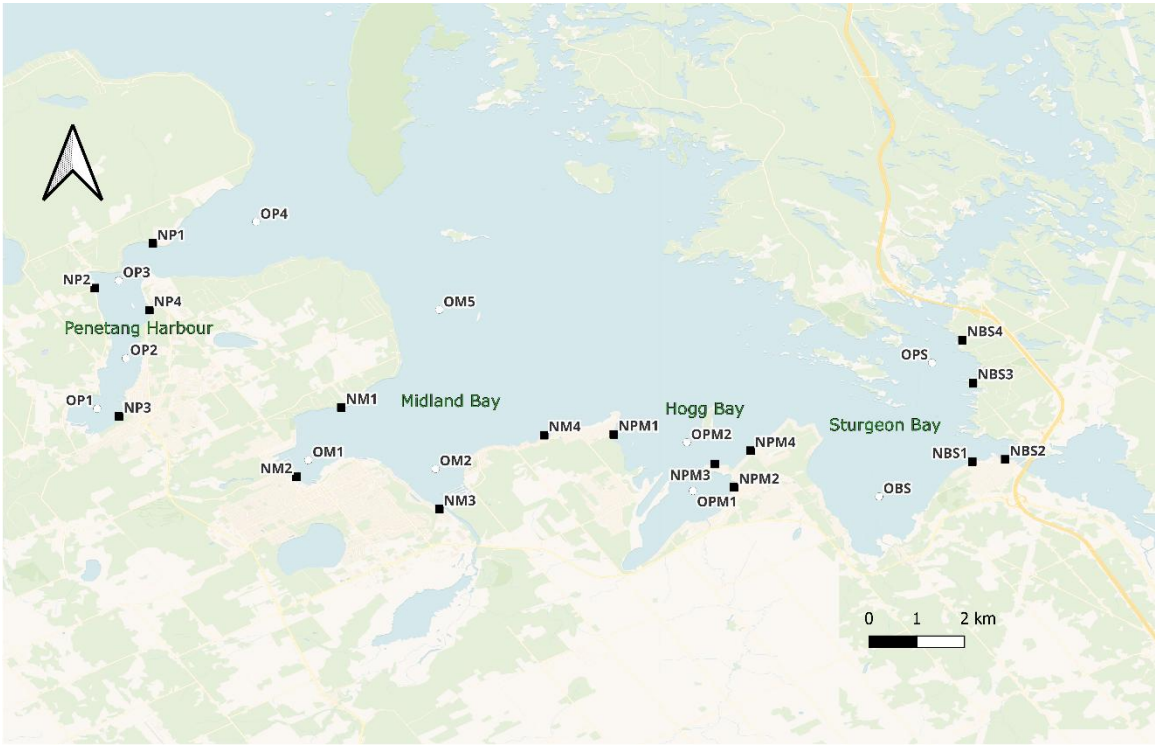

Figure 5.1. Sampling sites in Severn Sound. Nearshore sites (N) are indicated by black squares and offshore sites (O) are indicated by white circles.

5.2.2 Nearshore sample collection

Field data and water samples were taken at each nearshore site at a standardized standing depth of 1m and collected at 30cm below the surface. Field measurements of dissolved oxygen (mg/L), temperature (°C), specific conductivity (µS/cm), and pH were

taken with a 650 MDS multi parameter probe (YSI Inc., Yellow Springs, Ohio, USA). Water samples were collected in two 1-L acid washed Nalgene bottles and one sterile urine specimen cup. Samples were kept in a cooler with ice during transit and kept refrigerated until lab processing.

Water samples were processed within 24 hours of collection. A sub-sample of water (300mL) was filtered through 47mm GF/A glass fibre filters and the algal lawn was extracted for chlorophyll a using a 90% acetone extraction method followed by colorimetric spectrophotometry (Kirkwood et al., 1999). Water samples from the sterile specimen cups were used to determine total coliforms (TCol) and *Escherichia coli* (*Ecoli*) using Coliplates^{TM} (Bluewater Biosciences, Mississauga, ON). Water sub-samples (25mL) were sent to an accredited analytical laboratory for nitrogen suite analysis (NH3 + NH4, NO2, NO3, and total Kjeldahl nitrogen) (SGS Canada, Lakefield, Ontario). Total organic nitrogen (TON) was calculated by subtracting NH3+NH4 from total Kjeldahl nitrogen. Remaining water sub-samples (40mL) were used for TP and Total Dissolved Phosphorus (TDP) analyses. Samples allocated for TP were unfiltered and frozen in acid-washed falcon tubes until analysis. Samples allocated for TDP were first filtered through 0.2µm Whatman nylon membrane filters (GE Healthcare, Chicago, IL, USA) prior to freezing until analysis. Both TP and TDP samples were determined using a modified ascorbic acid method (Murphy & Riley, 1962) developed by the Ontario Ministry of the Environment (1983).

5.2.3 Offshore collection

Environmental parameters including Cond, TAN, TNN, TON, TN, TP, pH, Chla, and WT were collected as discussed in Chapter 2. Chlorophyll *a* was not analyzed across

all offshore sites, particularly OM2, P3, and PM1, due to resource limitations according to SSEA. Some sites, particularly OM2 in July and OBS in August, are missing parameters pH, Cond, and WT.

5.3.4 Statistical analysis

All statistical analyses were performed in the open-sourced software R version 4.4.0 (R Core Team, 2024). Some parameters did not follow normal distribution even with common transformations, so non-parametric statistical analyses were conducted when appropriate. Water temperature was normal without transformation, TON and TN were normal with a log transformation, and TP was normal with an inverse transformation. It is important to note that because the field and water chemistry samples were performed by different teams of people and labs, I elected to compare nearshore and offshore data using non-parametric statistical tests on ranks to remove absolute value comparisons and account for differences in measurement error. Data below detection limits were substituted for half the detection limit to reduce bias while allowing for statistical analysis. This approach is commonly used when non-detects comprise a small portion of the dataset and when the exact distribution of censored values is unknown.

To assess differences in nearshore and offshore water quality, each parameter was assessed using the Wilcox rank-sum test. Principal Component Analysis and PERMANOVA (999 permutations) based on Bray-Curtis dissimilarity were conducted using the *vegan* package (Oksanen et al., 2024) to compare nearshore and offshore water quality profiles as well as assess differences among embayments. To evaluate differences in water quality parameters among embayments, linear mixed-effects models (LMM) were fit using the *lme4* package, with Site included as a random effect to account for

spatial clustering (Bates et al., 2015). When models showed evidence of singular fits, standard linear models (LM) were used. Post-hoc comparisons were conducted using estimated marginal means with Tukey adjustments for multiple comparisons using the *emmeans* package (Lenth, 2025).

5.3 Results

Water quality differed significantly ($p<0.05$) between nearshore and offshore sites for most parameters, with some exceptions (Table 5.1). Mean TP, Chla, and Cond were significantly higher at the nearshore when compared to offshore sites. The nearshore also exhibited significantly higher TAN. In contrast, nitrogen forms TON, TNN, and TN were generally higher at offshore sites, although only TON differed significantly between regions. Mean WT and pH were similar between nearshore and offshore sites and were not significantly different. Variability, measured as standard deviation was consistently greater at nearshore sites compared to offshore sites for all parameters.

Table 5.1. Water Quality in the nearshore and offshore of Severn Sound during summer (June-September) 2022. Nearshore samples were collected by Ontario Tech University and offshore samples were collected by SSEA. T-tests were run Wilcoxon rank-sum test. No t-test was conducted on parameters only collected in the nearshore. Statistically significant p-value<0.05 is bolded.

Parameter	Region	n	min	max	mean	sd	p-value
Chla	Nearshore	16	2.44	113.66	12.76	27.15	**<0.001**
	Offshore	8	0.02	2.82	1.66	1.06	
Cond	Nearshore	16	363.53	604.08	433.58	65.73	**<0.001**
	Offshore	11	217.67	279	236.89	17.9	
pH	Nearshore	16	7.163	8.24	7.97	0.25	0.537
	Offshore	11	7.9	8.61	8.09	0.22	
TAN	Nearshore	16	20	65	35	13.13	**<0.001**
	Offshore	11	11.7	14.25	12.85	0.89	
TNN	Nearshore	16	3	72.5	24.8	19.34	0.645
	Offshore	11	9.7	42.8	25.93	11.33	
TON	Nearshore	16	225	492.5	293.59	61.91	**0.025**
	Offshore	11	283.3	377.2	321.93	31.77	
TN	Nearshore	16	264.25	555.5	353.39	70.72	0.451
	Offshore	11	335.5	402.95	360.7	22.18	
TP	Nearshore	16	33.31	273.14	54.52	58.53	**<0.001**
	Offshore	11	9.38	14.01	11.85	1.62	
WT	Nearshore	16	21.35	25	23.05	1.13	0.145
	Offshore	11	21.4	23.4	22.32	0.59	
DO	Nearshore	16	3.36	9.09	8.19	1.34	
Ecoli	Nearshore	16	3	269.5	31.39	65.68	
TDP	Nearshore	16	1.83	5.58	3.85	1.18	
Tcol	Nearshore	16	15.5	549.75	78.31	128.91	

To explore water quality profiles in the nearshore and offshore, a PCA was performed (Figure 5.2). The first principal component (PC1) explained 47.27% of the variance, while the second principal component (PC2) explained 25.11%. Nearshore data had much more variability when compared to the offshore. Nitrogen forms TN and TON were strongly positively correlated with each other and moderately positively correlated with TNN, Chla, and TP and moderately negatively correlated with WT and Cond. Total

phosphorus and Chla strongly positively correlated and moderately positively correlated with TAN, TN, and TON, and negatively correlated with pH. The offshore dataset strongly positively correlated with TNN and moderately positively correlated with TN and TON. The offshore dataset also moderately negatively correlated with WT, Cond, TAN, TP, and Chla. A PERMANOVA was run to determine if there was a difference in nearshore and offshore water quality and in the embayments of Severn Sound. Nearshore and offshore water quality was significantly different (F = 20.44, p-value <0.05), but embayments were not significantly different (F = 1.77, p-value = 0.113) and there was not a significant interaction in Region:Embayment (F = 0.65, p-value 0.695) (Table 5.2).

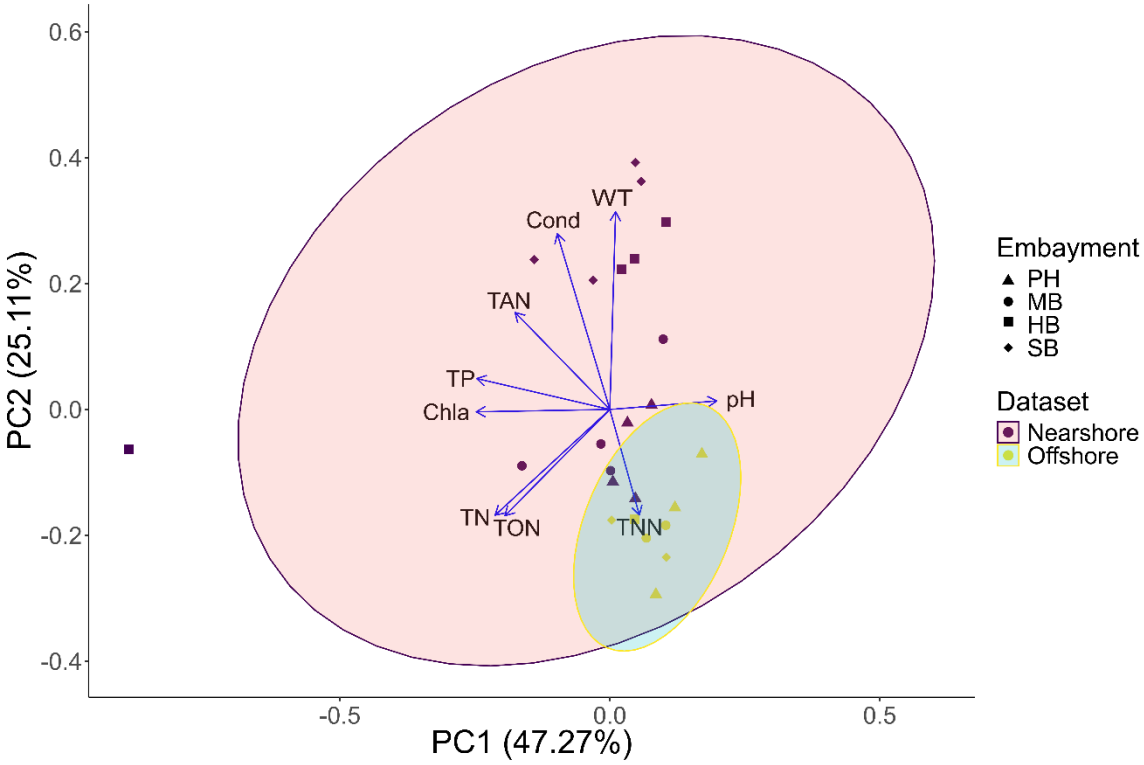

Figure 5.2. Principal Component Analysis of water quality parameters collected in Severn Sound nearshore and offshore sites from June-September 2022. Embayments include PH: Penetang Harbour, MB: Midland Bay, HB: Hogg Bay, and SB: Sturgeon Bay.

Table 5.2. Permutational Multivariate Analysis of Variance (PERMANOVA) of site averaged water quality parameters from Severn Sound (June-September 2022), comparing region (nearshore and offshore) and embayment (Penetang Harbour, Midland Bay, Hogg Bay, and Sturgeon Bay). The model tested differences using Bray-Curtis dissimilarity. Significant p-values are bolded.

Variance Index	Df	R^2	F-value	p-value
Region	1	0.468	20.44	**<0.001**
Embayment	3	0.122	1.77	0.113
Region:Embayment	3	0.045	0.65	0.695
Residual	16	0.366		

Linear Mixed-effect and Linear Models showed that most of the water quality parameters were not significantly different across the embayments in both the nearshore (Table 5.3) and offshore regions (Table 5.4) of Severn Sound. Site-effect was a more prominent model term in the nearshore samples, indicating that site-level variability may be less influential in the offshore region. Water temperature and conductivity were the only two parameters in both the nearshore and offshore to have a significant difference (p-value<0.05) across the embayments. For both parameters and regions, Penetang Harbour and Midland Bay were similar and Sturgeon Bay was significantly different compared to those two embayments. Hogg Bay was similar to all sites, showing an overlap between both groups.

Table 5.3. Linear Mixed Effects Models comparing water quality parameters in the embayments: Penetang Harbour (PH), Midland Bay (MB), Hogg Bay (HB), and Sturgeon Bay (SB), in nearshore Severn Sound. Linear Models were run for Cond, TDP, WT, and TNN due to singularity. Post-hoc group only included for models with significantly different embayments. Letters indicate similarity in water quality parameter.

Parameter		Embayment			
		PH	MB	HB	SB
WT	Estimate	21.925	0.419	1.619	2.456
	Std. Error	0.434	0.613	0.613	0.613
	Post-hoc group	a	a	ab	b
pH	Estimate	8.083	-0.171	-0.345	0.073
	Std. Error	0.107	0.151	0.151	0.151
Cond	Estimate	379.856	22.6	48.844	143.456
	Std. Error	29.844	42.206	42.206	42.206
	Post-hoc group	a	a	ab	b
Chla	Estimate	5.744	-0.051	25.417	2.694
	Std. Error	13.869	19.613	19.613	19.613
TAN	Estimate	30	4.375	8.125	7.5
	Std. Error	7.103	10.045	10.045	10.045
TNN	Estimate	40.062	-1.062	-33.625	-26.375
	Std. Error	11.423	16.155	16.155	16.155
TON	Estimate	279.375	14.375	31.25	11.25
	Std. Error	34.002	48.086	48.086	48.086
TN	Estimate	5.771	0.045	0.026	0.042
	Std. Error	0.102	0.144	0.144	0.144
TP	Estimate	0.029	-0.002	-0.007	-0.006
	Std. Error	0.003	0.004	0.004	0.004
TDP	Estimate	3.941	0.178	-0.117	-0.407
	Std. Error	1.1	1.555	1.555	1.555
Ecoli	Estimate	5.5	10.188	70.875	22.5
	Std. Error	33.195	46.945	46.945	46.945
Tcol	Estimate	48.812	-13.5	112.375	19.125
	Std. Error	66.219	93.648	93.648	93.648
DO	Estimate	8.559	-0.188	-1.223	-0.076
	Std. Error	0.69	0.975	0.975	0.975

Table 5.4. Linear Mixed Effects Models comparing water quality parameters in the embayments: Penetang Harbour (PH), Midland Bay (MB), Hogg Bay (HB), and Sturgeon Bay (SB), in offshore Severn Sound. Linear Models were run for Chla, TAN, TNN, TON, TN, TP, WT due to singularity. Post-hoc group only included for models with significantly different embayments. Letters indicate similarity in water quality parameter.

Parameter		Embayment			
		PH	MB	HB	SB
WT	Estimate	22.483	-0.4	0.024	-0.256
	Std. Error	0.507	0.794	0.878	0.919
	Post-hoc group	a	a	ab	b
pH	Estimate	8.127	-0.175	-0.09	0.183
	Std. Error	0.108	0.163	0.184	0.184
Cond	Estimate	224.529	4.805	16.971	44.221
	Std. Error	3.494	5.255	5.943	5.943
	Post-hoc group	a	a	ab	b
Chla	Estimate	2.193	-0.728	0.322	-1.371
	Std. Error	1.071	1.764	2.141	1.693
TAN	Estimate	13.419	-0.694	-0.931	-1.169
	Std. Error	1.033	1.578	1.789	1.789
TNN	Estimate	36.45	-7.292	-21.812	-25.125
	Std. Error	9.604	14.67	16.634	16.634
TON	Estimate	297.831	6.944	47.181	74.919
	Std. Error	7.008	10.704	12.138	12.138
TN	Estimate	5.84	0.005	0.076	0.141
	Std. Error	0.028	0.043	0.049	0.049
TP	Estimate	0.095	-0.015	-0.021	0.005
	Std. Error	0.004	0.006	0.007	0.007

5.4 Discussion

Mean water quality parameters generally were in range with other studies conducted in Georgian Bay and the Great Lakes (Decatanzaro et al., 2009; Howell & Holeton, 2023; Yurista et al., 2016). Some parameters in this study were higher than generally seen such as nearshore and offshore conductivity, although offshore conductivity did fall within the upper range seen in other studies (Howell & Holeton,

2023). Chlorophyll *a* levels were similar in the offshore region, however, the nearshore Chla was much higher in this study. Nearshore TP was much higher than seen in some studies (Howell & Holeton, 2023; Yurista et al., 2016) but were more similar to values seen in the costal marshes of Georgian Bay (Decatanzaro et al., 2009). Some nearshore sites were situated in or around areas with wetland characteristics, such as emergent vegetation and murky, waterlogged conditions, which may account for elevated nutrients in this study. Higher nutrient concentrations may also be attributed to relatively shallow depths of both nearshore and offshore sites in this study, as shallower systems tend to experience great sediment-water interactions, enhanced nutrient recycling, and reduced dilution potential compared to deeper systems (Wetzel, 2001). This study used nearshore depths of less than 3ft compared to less than 30m and an offshore depth ranging from 2m – 20m compared to greater than 30m depth in other studies (Yurista et al., 2016).

This study observed spatial variation in several water quality parameters between nearshore and offshore sites. We found significantly different levels of Chla, TP, and cond in the nearshore and offshore regions which has been seen in similar studies across the Great Lakes (Yurista et al., 2016). In contrast, WT did not differ significantly between nearshore and offshore sites, which is also consistent with past research in the Great Lakes, including Lake Huron (Yurista et al., 2016). This study found no significant differences in TNN which differs from other areas in Lake Huron, but TNN was not significantly different in Lake Ontario (Yurista et al., 2016). Generally, nutrients are higher in the nearshore (Howell et al., 2016) due to direct watershed inputs, however we found some nitrogen forms, particularly TNN, TON, and TN, were higher in the offshore. This is similar to trends seen in some of the Great Lakes, including Lake Huron where

TNN was higher in the offshore (Yurista et al., 2016). Previous studies have reported a negative correlation between nitrate and Chla, attributed to nitrate assimilation by phytoplankton during periods of high productivity (Havens et al., 2012), which may explain higher nitrogen forms in the offshore with reduced Chla.

Water quality in nearshore zones is often characterized by greater spatial and temporal variability compared to offshore regions. This arises from dynamic inputs of tributary inflows, surface runoff, point-source discharges, and groundwater contributions, all of which can fluctuate significantly, particularly following precipitation events (Howell et al., 2014; Larson et al., 2016). In this study, nearshore water quality was consistently more variable than offshore water quality for all measured parameters. These patterns align with findings from across the Great Lakes, where Chla, TNN, TP, and Cond also show elevated variability in nearshore areas. Water temperature variance has also been shown to differ significantly between nearshore and offshore regions of Lake Huron, though not consistently across the Great Lakes (Yurista et al., 2016). The heightened variability observed in this study's nearshore sites is likely due to a combination of site-specific factors, including shallow depths, reduced mixing, and localized influenced such as tributary drainage. In addition, morphological features such as embayment enclosure and limited circulation can cause water to remain in nearshore zones for longer periods, amplifying the impact of localized inputs and leading to great temporal fluctuations. These characteristics help explain the observed differences between nearshore and offshore water quality dynamics in this system.

Principal component analysis and PERMANOVA confirm difference in overall water quality characteristics and variability in the nearshore versus offshore. The

nearshore region was much more variable and did not associate with certain parameters. Whereas the offshore region was much less variable and was associated with increased TNN, TON, TN, and pH. Although I found a difference in nearshore-offshore water quality in Severn Sound, the PCA and PERMANOVA did not find a significant difference in water quality across the embayments. Previous reports have suggested differences in water quality parameters such as TP, WT, nitrogen, and pH in Severn Sound embayments due to morphological characteristics, wastewater discharge, and plant community differences (Severn Sound Remedial Action Plan, 1988; Severn Sound Remedial Action Plan, 1993). These differences may not be as substantial anymore due to decreases in nutrients across Severn Sound and increases in water temperature.

Although overall water quality was not different across the embayments, linear and linear mixed-effects models indicated that certain parameters were significantly different, specifically conductivity and temperature. Sites in Sturgeon Bay differed from sites in Penetang Harbour and Midland Bay, while Hogg Bay overlapped with both. In the nearshore zone, both parameters were higher in Sturgeon Bay than Penetang Harbour. Conductivity may be influenced by inflow from Coldwater River that passes through a wetland embayment, Matchedash Bay adjacent to the study area, which may deliver ion-rich water to the Sturgeon Bay nearshore sites. Typical conductivities in freshwater lakes and streams are comparatively low, while wetlands can exhibit a much wider and in some cases much higher range of conductivity, which aligns with conditions observed at these sites (Yetter et al., 2014). Conductivity remained elevated in both nearshore and offshore zones of Sturgeon Bay, suggesting a consistent influence from upstream inputs or internal sources. Temperatures were higher in the nearshore of Sturgeon Bay, likely due to the

shallowness of the bay. However, offshore water temperature in Sturgeon Bay was lower than in Penetang Harbour, despite Sturgeon Bay's overall shallower depth. Although site BS is historically known for being warmer due to the shallowness of the embayment (Severn Sound Remedial Action Plan, 1988), site PS is also located in Sturgeon Bay with more open morphology and greater flushing, which enhances mixing and reduces heat accumulation and may increase lower average embayment temperatures. In contrast, Penetang Harbour is more enclosed with reduced water exchange which favors heat retention. Additionally, Chapter 2 noted that water temperature significantly increased only in Penetang Harbour over time which may explain why Sturgeon Bay is no longer warmer in the offshore.

Overall nearshore water quality conditions of Severn Sound are similar to costal wetlands in Georgian Bay with high nutrients and chla which is not surprising given the shallow sampling depth and wetland-like shorelines ((Decatanzaro et al., 2009; Howell & Holeton, 2023). Offshore nutrients were also higher in this study than other Great Lakes, which maybe attributed to embayment qualities such as shallow sampling depths and limited mixing due to morphological features (Yurista et al., 2016; Severn Sound Remedial Action Plan, 1988). However, elevated nutrient levels in Severn Sound are also likely influenced by legacy nutrient loading and ongoing anthropogenic impacts, as this system has a documented history of eutrophication (Severn Sound Remedial Action Plan, 1988; Severn Sound Remedial Action Plan, 1993; Sherman, 2002). Although limited differences in embayments were noted in this Chapter, previous Chapters (2-4) do note differences in embayment water quality and phytoplankton, especially pre-delisting. The lack of embayment differences found in this study may be due to only sampling a single

season, whereas the previous chapters focused on longer datasets. In addition, much effort was put in place to reduce high levels of nutrients and phytoplankton to become delisted, especially in certain embayments, which may mean that embayments no longer experience as much distinction in water quality compared to pre-delisting. In addition, differences in water quality characteristics in the embayments may have been masked by increased variability given that this dataset was much smaller than the other Chapters and that higher variability is generally seen in the nearshore and embayment regions (Howell et al., 2012; Yurista et al., 2016). The nearshore region of Severn Sound had higher conductivity, TP, and Chla, likely attributed to land use activity and shallowness (Kelly, 2009; Yurista et al., 2016), whereas the offshore region had higher TNN, TON, and TN, potentially due to less biological activity decreasing nitrogen assimilation by phytoplankton (Havens et al., 2012).

Coliform bacteria, including Tcol and Ecoli, were measured at nearshore sites to assess potential fecal contamination, which can indicate both public health risks and nutrient loading from fecal sources. Most nearshore sites in this study remained well below the Ontario provincial water quality objectives (PWQO) for recreational waters, 100 *E. coli* per 100mL and the historical threshold 1000 Tcol counts per 100mL (Ontario Ministry of the Environment, Conservation and Parks, 2021). However, one site in Hogg Bay in early summer exceeded both thresholds. Field observations at this site noted murky, waterlogged conditions and the presences of emergent vegetation and wildlife, suggesting saturated soils and wetland-like features. These characteristics may have contributed to higher levels of fecal contamination through increased wildlife activity or reduced dilution. Although no statistically significant differences were found among

embayments, these results highlight the potential influence of local environmental conditions on fecal indicator bacteria levels and supports the need for continued monitoring in nearshore areas with wetland features.

This study highlights significant spatial differences in nearshore and offshore zones within the delisted AOC, Severn Sound. Elevated concentrations of TP and Chla in the nearshore suggest higher primary productivity likely influenced by nutrient inputs from urban runoff, tributaries, or sediment resuspension. In contrast, the offshore sites exhibit lower TP and Chla and elevated nitrogen forms which may reflect reduced biological uptake, differences in water column mixing, or offshore nutrient regeneration. These findings suggest that nutrient cycling and limitation dynamics differ across the nearshore-offshore gradient, with potential implications for the design of monitoring programs and nutrient management strategies. Importantly, the observed offshore accumulation of nitrogen highlights the need to consider offshore processes in eutrophication assessments, which have traditionally focused on nearshore zones. A more integrated spatial approach may be necessary to effectively manage nutrient loading and meet remediation goals for AOCs in the Great Lakes.

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Chapter 6. General discussion and conclusions

My thesis aimed to address two main research goals: evaluate temporal and spatial trends in water quality and phytoplankton communities and assess drivers of the changes and differences. To achieve these goals, this research was guided by four research objectives: (1) Investigate the temporal and spatial variability in water quality within the embayments of Severn Sound and identify the environmental drivers underlying these patterns (Chapter 2), (2) assess long-term and spatial trends in phytoplankton biovolume and community composition in Severn Sound and determine the key factors influencing these dynamics (Chapter 3), (3) examine temporal and spatial shifts in cyanobacterial community composition and dynamics and evaluate the environmental drivers contributing to these changes in Severn Sound (Chapter 4), and (4) assess nearshore water quality in Severn Sound and compare with offshore water quality characteristics (Chapter 5). By addressing these research objectives in my doctoral research, I have been able to offer new insights on the ecological condition of Severn Sound through both an historical and management lens.

The long-term Severn Sound water quality dataset provided by SSEA revealed notable trends and shifts in water quality, phytoplankton, and cyanobacteria over several decades, while the nearshore study captured baseline data reflecting finer-scale nearshore water quality conditions. This multi-scale approach allowed for a more nuanced interpretation of how trends and patterns differed across temporal and spatial scales. It highlighted that ecosystem change is not uniform but varies significantly by location and time period, emphasizing the need for monitoring strategies that capture temporal and spatial variability and dynamics.

The insights gained from this research extends beyond Severn Sound and contributes to a broader understanding of nutrient dynamics and HAB development in freshwater embayment systems. Recognizing the temporal and spatial heterogeneity of these environments is essential for developing effective management and mitigation strategies, as it enables interventions that respond to shifting environmental conditions and local conditions. These results support the design of monitoring programs that balance the need to monitor long-term environmental change and maintain sufficient spatial detail. By identifying key drivers and patterns associated with bloom dynamics, this work can inform the development of predictive models and improve the targeting of future monitoring and management efforts. Ultimately this work underscores the importance of incorporating both temporal and spatial trends when assessing the health and resilience of freshwater systems.

6.1 Long-term trends in water quality and phytoplankton dynamics

Long-term ecological datasets are essential for understanding how aquatic ecosystems respond to environmental change, management interventions, and natural variability. In dynamic systems like Severn Sound, sustained monitoring enables the detection of trends that may unfold over decades and reveals whether observed changes reflect true ecosystem shifts versus short-term fluctuations. By examining over 40 years of water quality and phytoplankton data, this research provides critical insights into the ecological trajectory of the region following phosphorus abatement efforts and offers a valuable perspective on the persistence and evolution of eutrophic conditions.

Over several decades, Severn Sound has undergone pronounced changes in water quality, largely driven by nutrient reduction efforts and broader environmental shifts. Following the introduction of phosphorus controls in the late 1970s, TP concentrations declined across the region over the intervening decades (Table 2.2, Figure 2.5). This trend is consistent across the Great Lakes and in other regions of Lake Huron and aligns with both implementation of GLWQA nutrient reduction programs and upgrades to sewage treatment (Stadig et al., 2020, Bierman et al., 1984). These reductions in phosphorus have tangible results, with both Chla and Z_{SD} reductions being seen across most of the region suggesting improved water clarity and lower algal biomass, clear indicators of the effectiveness of phosphorus management strategies.

In contrast, nitrogen forms exhibited divergent trends. Results of nitrogen forms were much more variable with some species increasing such as TNN, while other such as TON and TN decrease, and even some species such as TAN experiencing differing trends across embayments (Table 2.2, Figure 2.4). Although these results show a high degree of variability, they are comparable to other trends seen in the Great Lakes regions, including increasing TNN, and TN increasing in the 1990s and then decreasing throughout the 2000s (DeBues et al., 2019; Stow et al., 2015). Nitrogen is more chemically labile than phosphorus and is more sensitive to biogeochemical processes and land use changes as it exists in multiple states and dissolved forms that cycle rapidly via biological uptake, mineralization, nitrification, and denitrification. These nitrogen trends likely reflect a combination of factors. Remedial actions in Severn Sound largely focused on reducing phosphorus, however, many of these interventions also influence the amounts and forms (speciation) of nitrogen entering the system. Efforts such as upgrading sewage treatment

plants, improving septic systems, reducing stormwater runoff, managing agricultural inputs, regulating black and grey water discharges from boats, and controlling erosion contribute to broader nutrient management outcomes (Severn Sound Remedial Action Plan, 1988; Severn Sound Remedial Action Plan, 1993; Sherman, 2002). For example, improvements to stormwater treatment infrastructure can alter nitrogen speciation by promoting a shift from organic to more bioavailable inorganic forms. Similarly, tributary rehabilitation initiatives, including livestock exclusion, riparian buffer restoration, and stream bank stabilization, not only reduce phosphorus inputs but also limit nitrogen runoff from agricultural areas. Upgrades to septic systems reduce leaching of nitrogen-rich effluent into groundwater and adjacent water bodies. Collectively, these measures play an important role in modifying both the quantity and bioavailability of nitrogen, influencing its cycling and ecological impacts in Severn Sound.

Among the long-term sampling stations in Severn Sound, only one site exhibited a statistically significant increase in water temperature since the 1970s, although many sites have shown a small positive trend in temperature, especially in more recent years. (Table 2.2, Figure 2.5, Figure A2). This aligns with broader research in the Great Lakes, which indicates that while some areas have experienced rising temperatures, others have no change or non-significant increases (Dobiesz & Lester, 2009; McCormick & Fahnenstiel, 1999). The only site experiencing significant warming is site P1, which is located in a narrow, semi-enclosed embayment with limited connection and exchange to the main basin, conditions that likely reduce flushing, weaken mixing, and promote enhanced heat retention (Shore, 2021; Wells and Sealock, 2009). In contrast, sites located in more open areas with more direct connectivity to the main channel are more exposed

to wind-driven mixing and interchange with the main basin, processes that can buffer local warming by dispersing accumulated heat. In addition, water temperature data used in the Mann-Kendall analysis was pooled across the sampling period and only includes data from May-September which may mask warming trends occurring outside the sampling period, when recent studies suggest climate-driven changes are particularly pronounced (Shattwel et al., 2019; Woolway et al., 2021). Although only one site in Severn Sound has warmed significantly to date, the general upward trend across the region, even if not yet statistically significant, raises concern. In a recovering AOC with a legacy of nutrient enrichment and eutrophication, rising temperatures may exacerbate internal loading and phytoplankton growth, potentially undermining past remediation efforts (Kong et al., 2023).

Together these patterns suggest a system in transition. While phosphorus control efforts have clearly improved water quality, and recent data show no significant increase in phosphorus levels, the variable nitrogen dynamics highlight emerging nutrient imbalances that could further affect future ecosystem responses, particularly in the context of climate change. The spatial variability in some nitrogen forms further underscores the importance of site-specific monitoring and the potential influence of localized drivers such as inflows, sediment processes, or land-based sources (Cundill et al., 2007; Tian et al., 2017; Zhang et al., 2024). Understanding these interrelated trends is critical for anticipating future changes in bloom dynamics and guiding adaptive management strategies in Severn Sound and similar ecosystems.

Water quality trends were mirrored by changes in phytoplankton communities, which have shifted markedly since the 1970s. Total phytoplankton biovolume

significantly decreased throughout the mid-1980s to the late 1990s (Figure 3.2). This decrease coincided with both changes to nutrient levels and the introduction of the invasive zebra mussels (Nicholls et al., 2002; Nicholls & Carney, 2011; Stefanoff et al., 2018). These two drivers likely acted through complementary mechanisms. Nutrient reductions imposed bottom-up constraints on algal growth, while zebra mussel filtration exerted top-down grazing pressure on phytoplankton biomass. Changes in each of the phytoplankton divisions were investigated and illustrated division-specific responses to environmental changes (Table 3.1, Figure 3.6). This highlighted how different taxa vary in their sensitivity to nutrient limitation, grazing pressure, and physical conditions.

In addition to temporal trends, I also found significant shifts in phytoplankton community composition before, during, and after AOC designation, as well as before and after the zebra mussel invasion (Figure 3.5, Table 3.2, Table 3.3). These compositional changes indicate that both nutrient regime shifts and biological invasion of zebra mussels played important roles in restructuring the phytoplankton assemblage (Reavie et al., 2025; Winter et al., 2011). Alterations in phytoplankton composition can cascade through the food web by changing the availability and quality of primary production to zooplankton and benthic grazers, thereby influencing higher trophic levels such as fish (Madenjian et al., 2015; Mooney et al., 2025).

Due to the potential environmental, human health, and economic impacts of HABs, I investigated the long-term changes to the cyanobacterial community in Severn Sound, including the toxigenic genera *Aphanizomenon*, *Dolichospermum*, and *Microcystis.* These taxa consistently dominated the community and similar to the broader phytoplankton community trends, the cyanobacterial community also experienced genus-

specific responses to environmental drivers (Figure 4.3, Table 4.4, Table 4.5, Table 4.6). These differences in community composition can be seen before and after delisting as an AOC (Table 4.1, Figure 4.1), as well as an association with *Aphanizomenon* pre-1990 and *Microcystis* post-1990 (Table 4.3). This change may reflect shifts in nutrient availability that favor *Microcystis*, as well as warming water temperatures and reduced grazing pressure due to zebra mussels, which selectively avoid this genus (Vanderploeg et al., 2001). Importantly, the rise of *Microcystis* post-1990 is notable given its frequent association with microcystin production (Yu et al., 2014). Overall, these patterns suggest cyanobacterial community composition in Severn Sound is being shaped by a combination of changing nutrient dynamics, climate change, and invasive species such as zebra mussels (Betros-Fortis et al., 2016; Bierman & Dolan, 1981; Dobiesz & Lester, 2009; Fisherman et al., 2010). Understanding these shifts is critical for anticipating bloom risk, early warning systems, and nutrient management strategies.

My findings highlight the complex and dynamic nature of water quality and phytoplankton responses in Severn Sound. While nutrient reductions have led to significant reductions in phosphorus concentrations and algal biomass, shifts in phytoplankton and cyanobacterial community composition and the start of increasing temperatures across the region suggest potential management concerns in the future. Overall, these results emphasize the importance of sustained and adaptive management.

6.2 Spatial heterogeneity in an embayment system

Spatial heterogeneity is an important feature of lake ecosystems, where differences in basin morphology, nutrient inputs, and hydrodynamic conditions create

localized environmental gradients that shape biological communities (Cao et al., 2023). In Severn Sound, spatial differences in water quality and phytoplankton dynamics are influenced by both morphology and anthropogenic pressures (Nicholls & Heintsch, 1992; Severn Sound Remedial Action Plan, 1988). Understanding these spatial patterns is essential for identifying localized drivers of eutrophication, designing effective management strategies, and improving management interventions. Spatial variability in water quality and phytoplankton was evident across Severn Sound, with differences both among embayments and between nearshore and offshore regions.

Long-term water quality data revealed both consistent system-wide patterns and notable spatial variability across monitoring stations. Friedman tests revealed that water quality parameters were mostly significantly different across stations, with some exceptions (Table 2.1). Trend analysis revealed similar long-term trends across stations, however, some parameters showed significant trends only at certain locations, underscoring localized dynamics (Table 2.2). In addition, while many parameters showed similar trends over time, significant differences among stations were also observed, specifically P1 exhibiting distinct clustering in multivariate analyses (Figure 2.2, Figure 2.3). Generalized Additive Mixed Models confirmed that station was a significant predictor for all water quality parameters, reinforcing the importance of spatial context when interpreting long-term environmental change (Table 2.3).

These findings align with broader evidence that embayment systems often exhibit spatial heterogeneity in water quality due to their distinct physical and biogeochemical characteristics. Features such as embayment geometry and bathymetry restrict water exchange and can lead to longer water residence times which enhances nutrient retention

and internal cycling (Shore, 2021). In addition, reduced flushing, localized inputs and internal nutrient recycling from lake sediment contribute to elevated and spatially variable nutrient concentrations (Ferguson & Eyre, 2010). Recognizing and accounting for this internal variability is critical for accurately interpreting long-term trends, understanding ecosystem function, and designing effective monitoring and management programs tailored to specific embayment conditions.

Phytoplankton biovolume and community composition also exhibited notable spatial variability across Severn Sound (Figure 3.1, Figure 3.3). While overall biomass has declined since the 1970s in response to nutrient management, station P1 remains slightly elevated, suggesting localized drivers are maintaining higher productivity. These patterns likely reflect factors such as site-specific nutrient inputs, reduced hydrodynamic mixing, or longer residence times that enhance nutrient retention and support sustained phytoplankton growth (Shen et al, 2022; Wang et al, 2018). Restricted exchange with the main basin causes prolonged water residence times, enhancing nutrient retention and internal cycling that results in elevated and spatially variable nutrient concentrations, thereby affecting phytoplankton community composition and abundance (Munawar et al., 2018). Differences in relative abundance of phytoplankton divisions were evident both historically and in recent years, with no convergence towards a uniform community structure (Figure 3.4). Instead, the dominant phytoplankton divisions shifted differently at each location, reflecting varied environmental pressures. Both GAMMs and PERMANOVA confirmed station as a significant predictor of phytoplankton biovolume and composition, with a significant interaction between station and time (Table 3.1, Table 3.2, Table 3.3). This suggests that spatially distinct communities are not only shaped by

local conditions but are also responding differently to long-term environmental changes. These findings highlight the importance of considering spatial context when assessing long-term ecological trends in embayment systems. Failing to account for within-system variability could obscure localized bloom risks or lead to ineffective management response that assume uniform conditions across stations.

Cyanobacterial communities in Severn Sound showed weaker spatial patterns compared to the overall phytoplankton community across sites, but spatial differences were still detectable. The PERMANOVA results indicated that station was a significant factor in shaping cyanobacterial composition, though the effect size was small relative to temporal variation (Table 4.1). The absence of a significant station by time interaction suggests temporal shifts in the cyanobacterial community, likely driven by broader environmental changes such as nutrient reductions and invasive species. However, species-specific modelling revealed that certain taxa, particularly *Dolichospermum* and *Microcystis*, exhibited spatially distinct patterns, with station emerging as a significant predictor in the GAMs (Table 4.4, Table 4.5, Table 4.6). This suggests that while overall cyanobacterial community is primarily shaped by long-term drivers, localized environmental conditions such as differences in nutrient dynamics, temperature, and clarity, may influence the dominance or bloom potential of specific genera.

These findings align with broader studies that show time was a more important factor for cyanobacterial communities than spatial dynamics, however, some areas with strong differences in nutrient dynamics have found more impacts from spatial dynamics (Rock et al., 2025; Wynne & Stumpf, 2015). This indicates that in ecosystems such as Severn Sound, spatial influences will be more important to the cyanobacterial community

due to the unique nutrient dynamics of the ecosystem. Recognizing this structure of temporal and spatial control is essential for understanding cyanobacterial community dynamics and anticipating site-specific bloom risks.

A focused spatial study in 2022 revealed marked differences between nearshore and offshore sites across several key water quality parameters. I found Chla, cond, TAN, and TP were significantly higher in the nearshore, whereas TON was significantly higher in the offshore. Other parameters including TNN, TN, WT, and pH showed no significant differences between regions (Table 5.1). Although TON was the only parameter significantly higher in the offshore, mean TNN and TN were also elevated in the offshore. Similar spatial gradients have been reported in the Great Lakes, where offshore waters often exhibited higher TNN concentration, although the magnitude and significance of these differences varied (Yurista et al., 2016). Water quality variability was higher in the nearshore region, consistent with other studies showing higher nutrients, productivity, and variability in nearshore zones, driven by proximity to inputs (Yurista et al., 2016). PERMANOVA indicated that nearshore and offshore locations significantly influenced overall water quality, while embayment identity did not, suggesting broad regional patterns such as shoreline nutrient loading or physical isolation of the nearshore zone may exert a stronger influence than embayment specific characteristics (Table 5.2). Linear mixed-effects models and linear model results showed that only WT and cond varied significantly across embayments in both nearshore and offshore zones, with no consistent embayment-level differences for other parameters (Table 5.3, Table 5.4). This suggests that during the 2022 sampling period, large-scale

spatial gradients were the dominant drivers of water quality patterns, while finer-scale variation among embayments was less pronounced.

However, interpreting these findings within the broader historical context is essential. Long-term analyses of this study show that both water quality and phytoplankton communities vary meaningfully across sites and that site-specific conditions can influence long-term trends and biological responses. While some parameters show system-wide trends, others display distinct local patterns, reinforcing the need for spatially explicit monitoring. The relatively limited embayment variation observed in 2022 may reflect specific seasonal or hydrological conditions rather than an absence of underlying spatial variability. Nearshore areas exhibit elevated nutrients and higher Chla, reflecting their role as zones of accumulation and biological activity. Together these findings emphasize that spatial heterogeneity, across embayments and nearshore-offshore zones, shapes ecosystem dynamics and must be accounted for in both research and management strategies. Recognizing this interaction is critical for designing robust monitoring programs and developing management strategies that are responsive to spatial variability in embayment systems. The spatial analyses conducted provide important insights into how localized conditions shape ecological dynamics within embayments and nearshore-offshore zones, and why spatial heterogeneity must be considered in monitoring and management. It is clear that spatial variability remains a critical aspect of ecosystem dynamics in Severn Sound.

6.3 Policy and management implications of long-term and spatial dynamics in Severn Sound

The comprehensive analysis of long-term trends and spatial variability in water quality, phytoplankton, and cyanobacteria communities in Severn Sound offers important guidance for resource managers and policymakers aiming to mitigate HABs and protect ecosystem health. By integrating data across decades and different spatial scales, including nearshore-offshore comparisons, this thesis provides a nuanced understanding of the drivers and persistence of bloom risk in this complex system.

One key implication is the need for sustained and spatially distributed monitoring programs. The observed significant spatial heterogeneity in water quality parameters and phytoplankton taxa across embayments and nearshore versus offshore sites demonstrates that no single location can adequately represent conditions across Severn Sound. This is particularly relevant for cyanobacterial taxa such as *Dolichospermum* and *Microcystis*, which show site specific patterns alongside temporal variability. Monitoring strategies should therefore prioritize a multi-site design that captures these spatial gradients, coupled with sufficient temporal frequency to detect seasonal and interannual changes. Such comprehensive monitoring enables more accurate bloom risk assessment and early warning, essential for timely management intervention (Cai et al., 2012; Paerl & Otten, 2013).

From a nutrient management perspective, the results indicate that phosphorus controls alone, while necessary, may be insufficient to fully prevent or reduce blooms in Severn Sound. The spatial and temporal decoupling observed between phosphorus concentrations and bloom occurrences suggests that a dual nutrient reduction strategy

targeting both phosphorus and nitrogen may be more effective (Baer et al., 2023). This aligns with emerging scientific consensus and regional management initiatives advocating for integrated nutrient targets to address complex drivers of eutrophication and HABs.

Moreover, the greater variability and increased TP and Chla in the nearshore emphasizes that these zones are hotspots for nutrient inputs and ecological processes influences by land use, hydrodynamics, and human activity (Blagrave et al., 2023). Therefore, management plans must incorporate nearshore environments as critical components of nutrient and bloom control strategies, recognizing that these areas often experience elevated nutrient concentrations, biological activity, and bloom formation risk compared to offshore waters (Yurista et al., 2016).

Climate change, particularly rising WT and increased nutrient loadings from intensifying rain events, poses a growing challenge for managing eutrophication and phytoplankton dynamics in freshwater systems like Severn Sound. Although increased WT has not been seen across the region, it is present in some areas and could be an emerging driver of increased bloom risk and shifts in community composition. Warmer conditions favour the proliferation of bloom-forming cyanobacteria such as *Microcystis*, which thrive under high temperatures and often exhibits increased toxicity and resilience in warmer waters (Paerl & Huisman, 2009). Elevated temperatures can also alter seasonal stratification, nutrient cycling, and grazing dynamics, indirectly influencing community structure and bloom timing (Carey et al., 2012). Temperature is not just a background variable, but a primary ecological driver that can amplify or override the effects of

nutrient management. As such, climate adaptation should be incorporated into monitoring and management frameworks.

In conclusion, this thesis highlights the importance of spatially explicit, long-term data to inform management of embayment systems like Severn Sound. Effective bloom prevention and water quality protection requires adaptive, multi-scale monitoring coupled with nutrient management approaches that address both phosphorus and nitrogen inputs and account for internal cycling processes. Continued investment in comprehensive monitoring across embayments and nearshore-offshore zones is essential to support these goals and enhance the resilience of freshwater ecosystems to eutrophication and HABs.

6.4 Study limitations and future directions

This study contributed valuable insights into spatial and temporal patterns in water quality and phytoplankton dynamics; however, several limitations should be acknowledged. The long-term dataset used in this study was primarily limited to collection during the summer months (May-October), a common constraint in lake monitoring programs due to accessibility and resource availability (Stanley et al., 2019). While summer sampling captures conditions during peak biological activity and is critical for assessing cyanobacterial blooms, this temporal limitation excludes other seasons in which significant changes in nutrient dynamics, stratification, and phytoplankton succession occur (Varga et al., 2024).

Furthermore, this study did not measure nutrient loadings, including point and non-points sources as well as internal loading, which can be a significant source of nutrients, especially in shallow systems (Orihel et al., 2017). Knowing where nutrients

were sourced from could have provided further context for interpreting spatially explicit nutrient dynamics over time. Additionally, this study lacked sufficient data on invasive species, particularly zebra mussels, which are known to alter nutrient cycling, water clarity, and phytoplankton community composition through direct filtration and indirect effects (Cha et al., 2011; Nicholls & Carney, 2011). Thus, I am only able to infer any role they played in changes in water quality, phytoplankton abundance and composition, and cyanobacteria abundance and community composition.

In addition, the long-term dataset reflects typical methodological variability associated with extended monitoring programs. Over the years, changes in water quality analytical techniques, such as TP and CHLA, have occurred and were accounted for to the extent possible. Phytoplankton taxonomic identification was performed by different analysts over time, however, SSEA did account for these differences by comparing the taxonomic work of different analysts with the same samples. This ensured that community composition was comparable over time, even with a small margin of methodological error. Additionally, due to time and financial constraints, biweekly phytoplankton samples were pooled at each site to represent annual means prior to taxonomic processing. This methodological approach restricted the ability to assess seasonal patterns in phytoplankton abundance and composition, which may have shed light on seasonal environmental drivers.

The nearshore-offshore dataset collected did not fall under a typical nearshore-offshore designation (Yurista et al., 2016), which may obscure the ability to compare to other studies. However, this provides an opportunity to investigate nearshore-offshore water quality in embayments that are generally excluded from these types of studies due

to their unique dynamics. Despite these limitations, this thesis provides a valuable contribution by linking long-term trends with spatial heterogeneity and highlights the need for integrated, multi-season and multi-process monitoring to fully understand phytoplankton and water quality dynamics in freshwater systems.

Building upon the findings and limitations of this study, several avenues for future research are recommended to enhance our understanding of long-term and spatial dynamics in water quality, phytoplankton, and cyanobacterial communities. First, expanding temporal coverage beyond the summer months is a critical next step. While summer sampling captures periods of peak biological activity, it over-looks transitional dynamics in spring and fall, and potentially understudied winter processes under ice cover. Year-round monitoring would allow for a more complete characterization of seasonal phytoplankton succession, nutrient availability, and bloom timing, which are increasingly influenced by changing climatic conditions.

Future work could also investigate interannual variability in both water quality and biological communities. Although long-term datasets provide a foundation for trend analysis, there remains a need to understand how year-to-year differences in nutrient inputs, temperature, and hydrology influence phytoplankton and cyanobacterial dynamics. Incorporating climate or watershed models could help contextualize biological variability in relation to broader environmental drivers. In addition, future work would benefit from investigating nutrient cycling processes. This could include assessing the role of internal loading from sediments, especially during periods of stratification or anoxia, as well as exploring nitrogen fixation and organic nitrogen pathways. These

processes can contribute substantially to nutrient availability and may sustain or exacerbate blooms under low external nutrient inputs.

Spatial dynamics also warrant further investigation. While this study provided an initial comparison of nearshore and offshore conditions, further research could apply spatially explicit models to evaluate whether nearshore conditions can be used to predict offshore dynamics or vice versa. This has potential for monitoring design and bloom forecasting. Additionally, repeating nearshore-offshore sampling across multiple seasons and years would help elucidate the temporal stability of spatial patterns, and how these relationships shift under varying environmental conditions. These future directions will help build a more comprehensive understanding of the ecological and biogeochemical processes shaping freshwater systems and improve the predictive capacity of management frameworks aimed at mitigating HABs and preserving water quality.

6.5 Final thoughts

Overall, my thesis investigated temporal and spatial trends in water quality, phytoplankton, and cyanobacteria in a delisted AOC, Severn Sound. The findings provide insight into the recovery of a previous AOC and offer a valuable reference to the remaining AOC with similar eutrophication-related challenges. My research shows significant changes in time of water quality, phytoplankton abundance and composition, and cyanobacteria abundance and composition. In addition, my research highlights the importance of spatial monitoring in Severn Sound and in other similar regions given the unique embayment and nearshore-offshore dynamics. This thesis contributes to a growing understanding of the spatial and temporal dynamics of water quality, phytoplankton, and cyanobacteria in freshwater systems. By integrating long-term monitoring data with

targeted nearshore-offshore sampling, it offers valuable insights into both broad-scale trends and finer-scale spatial variability.

Freshwater systems are increasingly shaped by complex interactions of nutrient input, biological interactions, land use, and climate change. As HABs continue to threaten water quality and ecosystem health, advancing our capacity to detect, predict, and manage these dynamics, both temporally and spatially, remains an urgent research priority.

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Appendix A

Chapter 2.

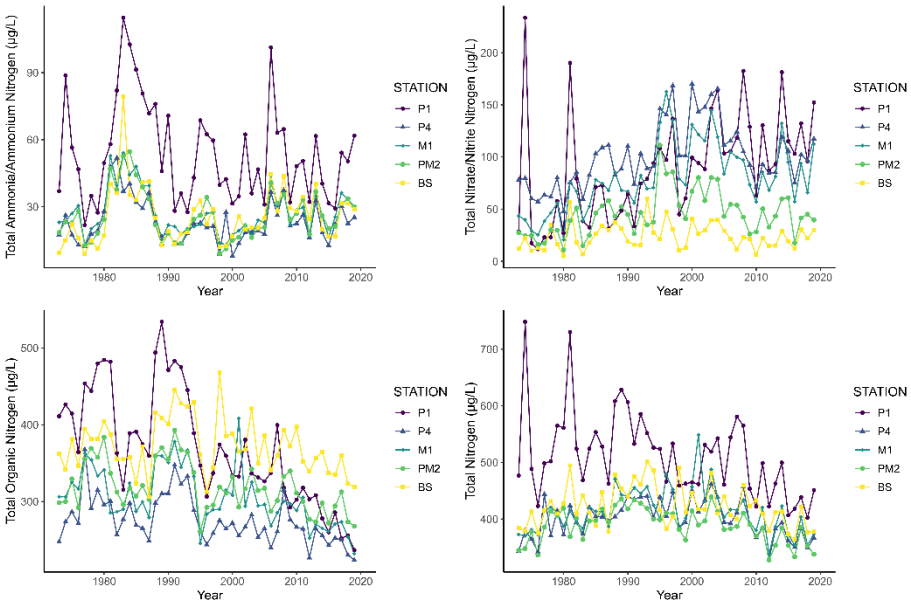

Figure A1. Yearly average of water quality parameters TAN, TNN, TON, TN at Severn Sound sampling stations from 1973-2020.

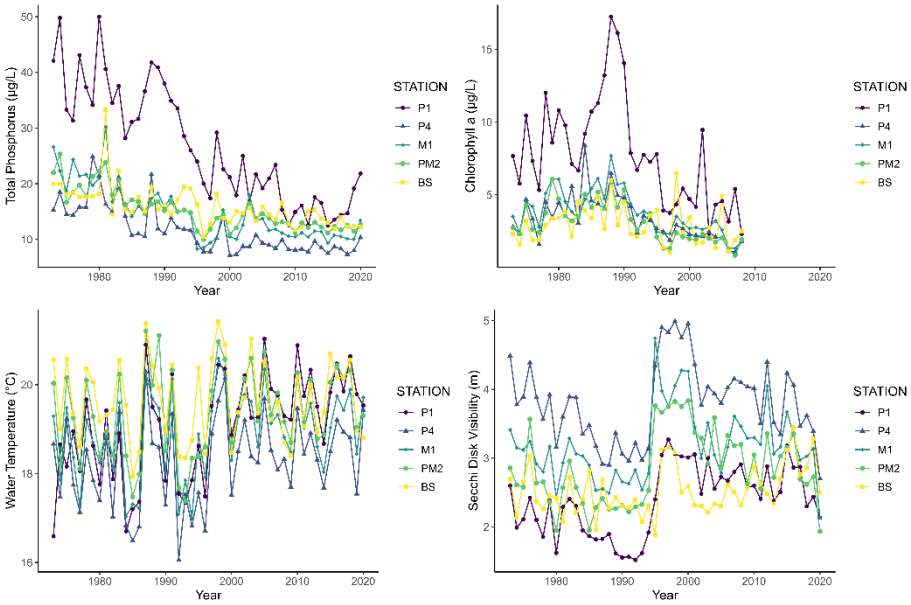

Figure A2. Yearly average of water quality parameters TP, Chla, WT, Z_{sd} at Severn Sound sampling stations from 1973-2020.

Table A1. AIC comparison for TAN GAMM for data collected 1973-2020. Best model bolded.

Model	Terms	AIC
M1	TAN ~ s(YEAR, k=47) + s(DOY, k=15), method="REML", family=tw	4967.45
M2	TAN ~ s(YEAR, k=47) + s(DOY, k=15)+ STATION, method="REML", family=tw	3996.74
M3	TAN ~ s(YEAR, k=47) + s(DOY, k=15) + STATION + s(WT), method="REML", family=tw	3996.73
M4	**TAN ~ s(YEAR, k=47) + s(DOY, k=15) + STATION, correlation = corARMA(form = ~1|YEAR,q=1)**	**3984.58**

Table A2. Summary table with smooth interaction terms for the final generalized additive mixed model of TAN in Severn Sound (n= 2186) from 1973-2020. Edf is the estimated degrees of freedom. Bolded p-values indicate statistical significance ($p < 0.05$).

Smooth terms	edf	F-value	p-value
s(YEAR)	34.8	17	**<0.05**
s(DOY)	4.5	24.2	**<0.05**
Parametric Coefficients	**Estimate**	**Standard Error**	**p-value**
P1	3.89	0.03	**<0.05**
P4	-0.83	0.04	**<0.05**
M1	-0.66	0.04	**<0.05**
PM2	-0.73	0.04	**<0.05**
BS	-0.72	0.04	**<0.05**
$R^2_{adjusted}$			0.43

Table A3. AIC comparison for TNN GAMM for data collected 1973-2020. Best model bolded.

Model	Terms	AIC
M1	TNN ~ s(YEAR, k=47) + s(DOY, k=15), method="REML", family=tw	6229.95
M2	TNN ~ s(YEAR, k=47) + s(DOY, k=15)+ STATION, method="REML", family=tw	5771.96
M3	TNN ~ s(YEAR, k=47) + s(DOY, k=15) + STATION + s(WT), method="REML", family=tw	5802.53
M4	**TNN ~ s(YEAR, k=47) + s(DOY, k=15) + STATION, correlation = corARMA(form = ~1|YEAR,q=1)**	**5764.86**

Table A4. Summary table with smooth interaction terms for the final generalized additive mixed model of TNN in Severn Sound (n= 2183) from 1973-2020. Edf is the estimated degrees of freedom. Bolded p-values indicate statistical significance ($p < 0.05$).

Smooth terms	edf	F-value	p-value
s(YEAR)	32.5	10.8	**<0.05**
s(DOY)	6.1	252	**<0.05**
Parametric Coefficients	**Estimate**	**Standard Error**	**p-value**
P1	4.14	0.04	**<0.05**
P4	0.23	0.06	**<0.05**
M1	-0.08	0.06	0.21
PM2	-0.71	0.06	**<0.05**
BS	-1.33	0.06	**<0.05**
$R^2_{adjusted}$			0.62

Table A5. AIC comparison for TON GAMM for data collected 1973-2020. Best model bolded.

Model	Terms	AIC
M1	TON ~ s(YEAR, k=47) + s(DOY, k=15), method="REML", family=tw	30.5974
M2	TON ~ s(YEAR, k=47) + s(DOY, k=15)+ STATION, method="REML", family=tw	-534.1
M3	TON ~ s(YEAR, k=47) + s(DOY, k=15) + STATION + s(WT), method="REML", family=tw	-530.69
M4	**TON ~ s(YEAR, k=47) + s(DOY, k=15) + STATION, correlation = corARMA(form = ~1|YEAR,p=1)**	**593.134**

Table A6. Summary table with smooth interaction terms for the final generalized additive mixed model of TON in Severn Sound (n = 2177) from 1973-2020. Edf is the estimated degrees of freedom. Bolded p-values indicate statistical significance ($p < 0.05$).

Smooth terms	edf	F-value	p-value
s(YEAR)	16.9	19.9	**<0.05**
s(DOY)	1	4.5	**<0.05**
Parametric Coefficients	**Estimate**	**Standard Error**	**p-value**
P1	5.89	0.01	**<0.05**
P4	-0.28	0.02	**<0.05**
M1	-0.17	0.02	**<0.05**
PM2	-0.14	0.02	**<0.05**
BS	0.02	0.02	0.22
$R^2_{adjusted}$			0.35

Table A7. AIC comparison for TN GAMM for data collected 1973-2020. Best model bolded.

Model	Terms	AIC
M1	TN ~ s(YEAR, k=47) + s(DOY, k=15), method="REML", family=tw	-493.25
M2	TN ~ s(YEAR, k=47) + s(DOY, k=15)+ STATION, method="REML", family=tw	-1091.8
M3	TN ~ s(YEAR, k=47) + s(DOY, k=15) + STATION + s(WT), method="REML", family=tw	-1121
M4	**TN ~ s(YEAR, k=47) + s(DOY, k=15) + STATION + s(WT), correlation = corARMA(form = ~1|YEAR,p=2)**	**-1215.1**

Table A8. Summary table with smooth interaction terms for the final generalized additive mixed model of TN in Severn Sound (n = 2174) from 1973-2020. Edf is the estimated degrees of freedom. Bolded p-values indicate statistical significance ($p < 0.05$).

Smooth terms	edf	F-value	p-value
s(YEAR)	7.9	16.8	**<0.05**
s(DOY)	5.2	68.5	**<0.05**
s(WT)	1	22.3	**<0.05**
Parametric Coefficients	**Estimate**	**Standard Error**	**p-value**
P1	6.22	0.01	**<0.05**
P4	-0.25	0.02	**<0.05**
M1	-0.21	0.02	**<0.05**
PM2	-0.27	0.02	**<0.05**
BS	-0.18	0.02	**<0.05**
$R^2_{adjusted}$			0.44

Table A9. AIC comparison for TP GAMM for data collected 1973-2020. Best model bolded.

Model	Terms	AIC
M1	TP ~ s(YEAR, k=47) + s(DOY, k=15), method="REML", family=tw	3113.22
M2	TP ~ s(YEAR, k=47) + s(DOY, k=15)+ STATION, method="REML", family=tw	1971.15
M3	TP~ s(YEAR, k=47) + s(DOY, k=15) + STATION + s(WT), method="REML", family=tw	1914.48
M4	**TP ~ s(YEAR, k=47) + s(DOY, k=15) + STATION +s(WT), correlation = corARMA(form = ~1|YEAR,q=2)**	**1882.526**

Table A10. Summary table with smooth interaction terms for the final generalized additive mixed model of TP in Severn Sound (n = 2223) from 1973-2020. Edf is the estimated degrees of freedom. Bolded p-values indicate statistical significance ($p < 0.05$).

Smooth terms	edf	F-value	p-value
s(YEAR)	13.1	51.7	**<0.05**
s(DOY)	8.4	10.3	**<0.05**
s(WT)	3.6	7.1	**<0.05**
Parametric Coefficients	**Estimate**	**Standard Error**	**p-value**
P1	3.2	0.02	**<0.05**
P4	-0.8	0.03	**<0.05**
M1	-0.55	0.03	**<0.05**
PM2	-0.52	0.03	**<0.05**
BS	-0.48	0.03	**<0.05**
$R^2_{adjusted}$			0.55

Table A11. AIC comparison for CHLA GAMM for data collected 1973-2008. Best model bolded.

Model	Terms	AIC
M1	CHLA ~ s(YEAR, k=36) + s(DOY, k=20), method="REML", family=tw	4184.67
M2	CHLA ~ s(YEAR, k=36) + s(DOY, k=20)+ STATION, method="REML", family=tw	3654.21
M3	CHLA ~ s(YEAR, k=36) + s(DOY, k=20) + STATION + s(TP) + s(WT) + s(TN), method="REML", family=tw	3164.84
M4	CHLA ~ s(YEAR, k=36)+s(DOY, k=20) + STATION + s(TP) + s(WT) + s(TON) + s(TAN) + s(TNN), method="REML", family=tw	2988.07
M5	CHLA ~ s(YEAR, k=36) + s(DOY, k=20) + STATION + s(TP)+ s(TON) + s(TAN) + s(TNN), method="REML", family=tw	2983.23
M6	**CHLA ~ s(YEAR, k=36) + s(DOY, k=20) + STATION + s(TP)+ s(TON) + s(TAN) + s(TNN), method="REML", family=tw, correlation = corARMA(form = ~1|YEAR,q=1)**	**2979.01**

Table A12. Summary table with smooth interaction terms for the final generalized additive mixed model of CHLA in Severn Sound (n = 1544) from 1973-2008. Edf is the estimated degrees of freedom. Bolded p-values indicate statistical significance ($p < 0.05$).

Smooth terms	edf	F-value	p-value
s(YEAR)	22	15.2	**<0.05**
s(DOY)	7.8	6.5	**<0.05**
s(TP)	5.5	6.7	**<0.05**
s(TON)	5.7	14.2	**<0.05**
s(TNN)	3.4	3	**<0.05**
s(TAN)	3.6	6.4	**<0.05**
Parametric Coefficients	**Estimate**	**Standard Error**	**p-value**
P1	1.6	0.05	**<0.05**
P4	-0.25	0.07	**<0.05**
M1	-0.27	0.06	**<0.05**
PM2	-0.57	0.06	**<0.05**
BS	-0.8	0.06	**<0.05**
$R^2_{adjusted}$			0.53

Table A13. AIC comparison for Z_{SD} GAMM for data collected 1973-2008.

Model	Terms	AIC
M1	ZSD ~ s(YEAR, k=36) + s(DOY, k=15), method="REML", family=tw	743.86
M2	ZSD ~ s(YEAR, k=36) + s(DOY, k=15)+ STATION, method="REML", family=tw	-110.91
M3	ZSD~ s(YEAR, k=36) + s(DOY, k=15) + STATION + s(chla), method="REML", family=tw	-436.76
M4	**ZSD ~ s(YEAR, k=36) + s(DOY, k=15) + STATION + s(chla), correlation = corARMA(form = ~1|YEAR,q=2)**	**-485.07**

Table A14. Summary table with smooth interaction terms for the final generalized additive mixed model of Z_{SD} in Severn Sound (n = 1686) from 1973-2008. Edf is the estimated degrees of freedom. Bolded p-values indicate statistical significance ($p < 0.05$).

Smooth terms	edf	F-value	p-value
s(YEAR)	15.6	17.9	**<0.05**
s(DOY)	7.4	30	**<0.05**
s(CHLA)	4.3	73.7	**<0.05**
Parametric Coefficients	**Estimate**	**Standard Error**	**p-value**
P1	0.93	0.01	**<0.05**
P4	0.38	0.02	**<0.05**
M1	0.21	0.02	**<0.05**
PM2	0.08	0.02	**<0.05**
BS	-0.08	0.02	**<0.05**
$R^2_{adjusted}$			0.63

Table A15. AIC comparison for WT GAMM for data collected 1973-2020.

Model	Terms	AIC
M1	WT ~ s(YEAR, k=47) + s(DOY, k=15), method="REML", family=tw	-3606.84
M2	WT ~ s(YEAR, k=47) + s(DOY, k=15)+ STATION, method="REML", family=tw	-3759.43
M3	WT ~ s(YEAR, k=47) + s(DOY, k=15) + STATION + s(ZSD), method="REML", family=tw	-3755.43
M4	**WT ~ s(YEAR, k=47) + s(DOY, k=15) + STATION, correlation = corARMA(form = ~1|YEAR,q=2)**	**-3877.11**

Table A16. Summary table with smooth interaction terms for the final generalized additive mixed model of WT in Severn Sound (n = 2291) from 1973-2020. Edf is the estimated degrees of freedom. Bolded p-values indicate statistical significance ($p < 0.05$).

Smooth terms	edf	F-value	p-value
s(YEAR)	27.3	7.6	**<0.05**
s(DOY)	10.5	823.2	**<0.05**
Parametric Coefficients	**Estimate**	**Standard Error**	**p-value**
P1	2.93	0.006	**<0.05**
P4	-0.05	0.008	**<0.05**
M1	-0.01	0.008	**<0.05**
PM2	0.01	0.008	0.22
BS	0.03	0.008	**<0.05**
$R^2_{adjusted}$			0.82

Appendix B

Chapter 3.

Table B1. Results of total biovolume (mm^3/m^3) GAMMs from 1973-2016. Best model bolded. Significant p-values are bolded (p-value <0.05).

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth		
			estimate	Std.	p-value	edf	F	p-value
Model 1	AIC = 276	Intercept	7.84	0.05	**<0.0001**			
	adj R^2 = 0.817	StationP4	-0.95	0.08	**<0.0001**			
	Family = tweedie	StationM1	-0.75	0.077	**<0.0001**			
		StationPM2	-1.13	0.082	**<0.0001**			
		StationBS	-1.43	0.086	**<0.0001**			
		s(Year,)				7.96	74.21	**<0.0001**
Model 2	AIC = 276	Intercept	7.83	0.049	**<0.0001**			
	adj R^2 = 0.823	StationP4	-0.98	0.08	**<0.0001**			
	Family = tweedie	StationM1	-0.75	0.076	**<0.0001**			
		StationPM2	-1.11	0.081	**<0.0001**			
		StationBS	-1.39	0.086	**<0.0001**			
		s(Year)				9.87	61.9	**<0.0001**
		s(WT)				1.44	1.99	0.088
Model 3	AIC = 261	Intercept	7.51	0.088	**<0.0001**			
	adj R^2 = 0.821	StationP4	-0.43	0.135	**0.0016**			
	Family = tweedie	StationM1	-0.37	0.113	**0.0012**			
		StationPM2	-0.76	0.117	**<0.0001**			
		StationBS	1.08	0.117	**<0.0001**			
		s(Year)				7.60	23.55	**<0.0001**
		s(TP)				2.25	9.34	**<0.0001**
Model 4	AIC = 249	Intercept	7.66	0.085	**<0.0001**			
	adj R^2 = 0.852	StationP4	-0.57	0.123	**<0.0001**			
	Family = tweedie	StationM1	-0.5	0.107	**<0.0001**			
		StationPM2	-0.98	0.117	**<0.0001**			
		StationBS	-1.35	0.123	**<0.0001**			
		s(Year)				13.3	19.17	**<0.0001**
		s(TP)				1.00	10.66	**0.001**
		s(TNN)				1.00	14.61	**0.0002**
Model 5	AIC = 245	Intercept	7.9	0.045	**<0.0001**			
	adj R^2 = 0.868	StationP4	-0.82	0.074	**<0.0001**			
		StationM1	-0.74	0.067	**<0.0001**			
		StationPM2	-1.32	0.076	**<0.0001**			
		StationBS	-1.76	0.096	**<0.0001**			
		s(Year)				16.1	30.97	**<0.0001**
		s(TNN)				2.83	11.29	**<0.0001**
Model 6	AIC = 235	Intercept	7.89	0.053	**<0.0001**			
	adj R^2 = 0.825	StationP4	-0.89	0.058	**<0.0001**			
	p = 1	StationM1	-0.75	0.074	**<0.0001**			
		StationPM2	-1.25	0.095	**<0.0001**			
		StationBS	-1.62	0.111	**<0.0001**			
		s(Year)				5.65	42.22	**<0.0001**
		s(TNN)				1.60	6.9	**0.0041**

Table B2. Results of Bacillariophyta biovolume (mm^3/m^3) GAMMs from 1973-2016. Best model bolded. Significant p-values are bolded (p-value <0.05).

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth terms		
			estimate	Std. error	p-value	edf	F	p-value
Model 1	AIC = 438	Intercept	6.933	0.074	**<0.0001**			
	adj R^2 = 0.696	StationP4	-0.530	0.110	**<0.0001**			
	Family = tweedie	StationM1	-0.381	0.108	**0.0005**			
		StationPM2	-0.968	0.117	**<0.0001**			
		StationBS	-1.998	0.140	**<0.0001**			
		s(Year)				6.206	64.700	**<0.0001**
Model 2	AIC = 441	Intercept	6.931	0.074	**<0.0001**			
	adj R^2 = 0.69	StationP4	-0.557	0.112	**<0.0001**			
	Family = tweedie	StationM1	-0.386	0.108	**0.0004**			
		StationPM2	-0.954	0.118	**<0.0001**			
		StationBS	-1.972	0.142	**<0.0001**			
		s(Year)				6.416	57.634	**<0.0001**
		s(WT)				1.000	1.148	0.2850
Model 3	AIC = 432	Intercept	6.686	0.129	**<0.0001**			
	adj R^2 = 0.683	StationP4	-0.167	0.189	0.3790			
	Family = tweedie	StationM1	-0.088	0.164	0.5945			
		StationPM2	-0.668	0.173	**0.0001**			
		StationBS	-1.717	0.185	**<0.0001**			
		s(Year)				5.913	27.750	**<0.0001**
		s(TP)				1.000	5.384	**0.0213**
Model 4	AIC = 420	Intercept	7.000	0.073	**<0.0001**			
	adj R^2 = 0.702	StationP4	-0.467	0.107	**<0.0001**			
	Family = tweedie	StationM1	-0.412	0.103	**<0.0001**			
		StationPM2	-1.121	0.119	**<0.0001**			
		StationBS	-2.236	0.149	**<0.0001**			
		s(Year)				6.177	47.990	**<0.0001**
		s(TNN)				1.000	11.530	**0.0008**
Model 5	AIC = 417	Intercept	6.782	0.128	**<0.0001**			
	adj R^2 = 0.697	StationP4	-0.155	0.182	0.3980			
	Family = tweedie	StationM1	-0.156	0.160	0.3300			
		StationPM2	-0.853	0.175	**<0.0001**			
		StationBS	-1.980	0.195	**<0.0001**			
		s(Year)				5.886	25.540	**<0.0001**
		s(TP)				1.000	4.250	**0.0405**
		s(TNN)				1.000	11.080	**0.0010**
Model 6	AIC = 381	Intercept	6.763	0.123	**<0.0001**			
	adj R^2 = 0.696	StationP4	-0.144	0.163	0.3790			
	Family = tweedie	StationM1	-0.129	0.149	0.3850			
	p = 1	StationPM2	-0.808	0.167	**<0.0001**			
		StationBS	-1.922	0.188	**<0.0001**			
		s(Year)				3.882	22.933	**<0.0001**
		s(TP)				1.000	5.235	**0.0231**
		s(TNN)				1.000	8.050	**0.0050**

Table B3. Results of Chlorophyta biovolume (mm^3/m^3) GAMMs from 1973-2016. Best model bolded. Significant p-values are bolded (p-value <0.05).

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth terms		
			estimate	Std. error	p-value	edf	F	p-value
Model 1	AIC = 604	Intercept	5.444	0.099	**<0.0001**			
	adj R^2 = 0.533	StationP4	-1.479	0.171	**<0.0001**			
	Family = tweedie	StationM1	-1.437	0.170	**<0.0001**			
		StationPM2	-1.509	0.172	**<0.0001**			
		StationBS	-1.286	0.166	**<0.0001**			
		s(Year)				7.443	16.760	**<0.0001**
Model 2	AIC = 614	Intercept	5.431	0.100	**<0.0001**			
	adj R^2 = 0.611	StationP4	-1.384	0.177	**<0.0001**			
	Family = tweedie	StationM1	-1.406	0.172	**<0.0001**			
		StationPM2	-1.547	0.175	**<0.0001**			
		StationBS	-1.351	0.172	**<0.0001**			
		s(Year)				7.745	16.433	**<0.0001**
		s(WT)				1.000	4.966	**0.0269**
Model 3	AIC = 580	Intercept	5.094	0.171	**<0.0001**			
	adj R^2 = 0.589	StationP4	-0.880	0.276	**0.0017**			
	Family = tweedie	StationM1	-1.055	0.230	**<0.0001**			
		StationPM2	-1.151	0.232	**<0.0001**			
		StationBS	-0.989	0.222	**<0.0001**			
		s(Year)				8.443	10.115	**<0.0001**
		s(TP)				2.631	4.376	**0.0065**
Model 4	AIC = 595	Intercept	5.516	0.101	**<0.0001**			
	adj R^2 = 0.544	StationP4	-1.416	0.170	**<0.0001**			
	Family = tweedie	StationM1	-1.463	0.166	**<0.0001**			
		StationPM2	-1.664	0.180	**<0.0001**			
		StationBS	-1.531	0.191	**<0.0001**			
		s(Year)				6.572	14.240	**<0.0001**
		s(TNN)				1.000	5.490	**0.0201**
Model 5	AIC = 583	Intercept	5.017	0.171	**<0.0001**			
	adj R^2 = 0.631	StationP4	-0.685	0.278	**0.0148**			
	Family = tweedie	StationM1	-0.948	0.229	**<0.0001**			
		StationPM2	-1.121	0.231	**<0.0001**			
		StationBS	-1.001	0.221	**<0.0001**			
		s(Year)				9.422	11.040	**<0.0001**
		s(TP)				2.587	4.913	**0.0101**
		s(WT)				1.000	7.692	**0.0310**
Model 6	AIC = 578	Intercept	5.217	0.184	**<0.0001**			
	adj R^2 = 0.604	StationP4	-0.958	0.275	**0.0006**			
	Family = tweedie	StationM1	-1.155	0.235	**<0.0001**			
		StationPM2	-1.347	0.257	**<0.0001**			
		StationBS	-1.241	0.265	**<0.0001**			
		s(Year)				8.611	9.670	**<0.0001**
		s(TP)				2.397	3.429	**0.0339**
		s(TNN)				1.000	2.998	0.0849
Model 7	AIC = 583	Intercept	5.134	0.184	**<0.0001**			
	adj R^2 = 0.704	StationP4	-0.763	0.279	**0.0068**			
	Family = tweedie	StationM1	-1.044	0.235	**<0.0001**			
		StationPM2	-1.302	0.256	**<0.0001**			
		StationBS	-0.233	0.264	**<0.0001**			
		s(Year)				9.502	10.432	**<0.0001**
		s(TP)				2.381	3.808	**0.0238**
		s(TNN)				1.000	2.574	0.1102
		s(WT)				1.000	7.496	**0.0067**

Table B4. Results of Chrysophyta biovolume (mm^3/m^3) GAMMs from 1973-2016. Best model bolded. Significant p-values are bolded (p-value <0.05).

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth terms		
			estimate	Std. error	p-value	edf	F	p-value
Model 1	AIC = 471	Intercept	5.333	0.085	**<0.0001**			
	adj R^2 = 0.249	StationP4	-0.989	0.138	**<0.0001**			
	Family = tweedie	StationM1	-1.021	0.138	**<0.0001**			
		StationPM2	-0.891	0.136	**<0.0001**			
		StationBS	-0.604	0.130	**<0.0001**			
		s(Year)				3.818	7.636	**<0.0001**
Model 2	AIC =475	Intercept	5.333	0.085	**<0.0001**			
	adj R^2 = 0.248	StationP4	-1.012	0.141	**<0.0001**			
	Family = tweedie	StationM1	-1.027	0.139	**<0.0001**			
		StationPM2	-0.882	0.136	**<0.0001**			
		StationBS	-0.584	0.132	**<0.0001**			
		s(Year)				3.786	7.453	**<0.0001**
		s(WT)				1.000	0.486	0.4860
Model 3	AIC = 469	Intercept	5.446	0.133	**<0.0001**			
	adj R^2 = 0.287	StationP4	-1.131	0.215	**<0.0001**			
	Family = tweedie	StationM1	-1.166	0.183	**<0.0001**			
		StationPM2	-1.046	0.179	**<0.0001**			
		StationBS	-0.763	0.171	**<0.0001**			
		s(Year)				4.035	8.711	**<0.0001**
		s(TP)				2.019	3.041	**0.0475**
Model 4	AIC = 469	Intercept	5.207	0.092	**<0.0001**			
	adj R^2 = 0.288	StationP4	-0.999	0.135	**<0.0001**			
	Family = tweedie	StationM1	-0.945	0.138	**<0.0001**			
		StationPM2	-0.668	0.149	**<0.0001**			
		StationBS	-0.301	0.159	0.0601			
		s(Year)				4.144	10.340	**<0.0001**
		s(TNN)				1.000	11.020	**0.0011**
Model 5	AIC = 464	Intercept	5.182	0.145	**<0.0001**			
	adj R^2 = 0.397	StationP4	-0.957	0.217	**<0.0001**			
	Family = tweedie	StationM1	-0.949	0.185	**<0.0001**			
		StationPM2	-0.657	0.200	**0.0012**			
		StationBS	-0.284	0.209	0.1754			
		s(Year)				4.520	10.878	**<0.0001**
		s(TP)				2.763	3.103	**0.0189**
		s(TNN)				1.000	13.382	**0.0003**
Model 6	AIC = 456	Intercept	5.183	0.149	**<0.0001**			
	adj R^2 = 0.383	StationP4	-0.943	0.213	**<0.0001**			
	Family = tweedie	StationM1	-0.935	0.187	**<0.0001**			
	p = 1	StationPM2	-0.646	0.204	**0.0018**			
		StationBS	-0.291	0.213	0.1736			
		s(Year)				3.646	6.652	**0.0001**
		s(TP)				2.464	2.492	**0.0460**
		s(TNN)				1.000	11.110	**0.0010**

Table B5. Results of Cryptophyta biovolume (mm^3/m^3) GAMMs from 1973-2016. Best model bolded. Significant p-values are bolded (p-value <0.05).

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth terms		
			estimate	Std. error	p-value	edf	F	p-value
Model 1	AIC = 675	Intercept	6.343	0.058	**<0.0001**			
	adj R^2 = 0.765	StationP4	-1.676	0.103	**<0.0001**			
	Family = tweedie	StationM1	-1.104	0.093	**<0.0001**			
		StationPM2	-1.443	0.099	**<0.0001**			
		StationBS	-1.573	0.101	**<0.0001**			
		s(Year)				5.633	72.010	**<0.0001**
Model 2	AIC = 361	Intercept	6.335	0.056	**<0.0001**			
	adj R^2 = 0.782	StationP4	-1.725	0.102	**<0.0001**			
	Family = tweedie	StationM1	-1.113	0.091	**<0.0001**			
		StationPM2	-1.410	0.097	**<0.0001**			
		StationBS	-1.516	0.101	**<0.0001**			
		s(Year)				5.827	64.060	**<0.0001**
		s(WT)				1.000	6.842	**0.0096**
Model 3	AIC = 355	Intercept	6.166	0.103	**<0.0001**			
	adj R^2 = 0.825	StationP4	-1.372	0.169	**<0.0001**			
	Family = tweedie	StationM1	-0.904	0.136	**<0.0001**			
		StationPM2	-1.255	0.140	**<0.0001**			
		StationBS	-1.401	0.138	**<0.0001**			
		s(Year)				5.959	25.221	**<0.0001**
		s(TP)				3.310	3.493	**0.0091**
Model 4	AIC = 366	Intercept	6.331	0.061	**<0.0001**			
	adj R^2 = 0.763	StationP4	-1.682	0.104	**<0.0001**			
	Family = tweedie	StationM1	-1.096	0.094	**<0.0001**			
		StationPM2	-1.419	0.107	**<0.0001**			
		StationBS	-1.539	0.117	**<0.0001**			
		s(Year)				5.297	64.668	**<0.0001**
		s(TNN)				1.000	0.332	0.5650
Model 5	AIC = 346	Intercept	6.159	0.101	**<0.0001**			
	adj R^2 = 0.834	StationP4	-1.413	0.167	**<0.0001**			
	Family = tweedie	StationM1	-0.912	0.134	**<0.0001**			
		StationPM2	-1.226	0.138	**<0.0001**			
		StationBS	-1.351	0.137	**<0.0001**			
		s(Year)				5.577	26.375	**<0.0001**
		s(TP)				3.328	3.654	**0.0079**
		s(WT)				1.000	6.275	**0.0130**

Table B6. Results of Cyanophyta biovolume (mm^3/m^3) GAMMs from 1973-2016. Best model bolded. Significant p-values are bolded (p-value <0.05).

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth terms		
			estimate	Std. error	p-value	edf	F	p-value
Model 1	AIC = 675	Intercept	4.815	0.135	**<0.0001**			
	adj R^2 = 0.219	StationP4	-1.145	0.222	**<0.0001**			
	Family = tweedie	StationM1	-0.951	0.215	**<0.0001**			
		StationPM2	-0.748	0.209	**<0.0001**			
		StationBS	-0.384	0.198	0.0537			
		s(Year)				4.735	14.560	**<0.0001**
Model 2	AIC = 681	Intercept	4.814	0.136	**<0.0001**			
	adj R^2 = 0.215	StationP4	-1.160	0.227	**<0.0001**			
	Family = tweedie	StationM1	-0.955	0.216	**<0.0001**			
		StationPM2	-0.741	0.211	**0.0006**			
		StationBS	-0.367	0.204	0.0738			
		s(Year)				4.735	13.690	**<0.0001**
		s(WT)				1.000	0.104	0.7470
Model 3	AIC = 640	Intercept	4.083	0.215	**<0.0001**			
	adj R^2 = 0.248	StationP4	-0.111	0.320	0.7300			
	Family = tweedie	StationM1	-0.106	0.282	0.7080			
		StationPM2	0.102	0.280	0.7150			
		StationBS	0.431	0.265	0.1060			
		s(Year)				4.500	5.388	**0.0002**
		s(TP)				1.000	17.789	**<0.0001**
Model 5	AIC = 664	Intercept	4.897	0.135	**<0.0001**			
	adj R^2 = 0.255	StationP4	-1.040	0.218	**<0.0001**			
	Family = tweedie	StationM1	-0.956	0.208	**<0.0001**			
		StationPM2	-0.964	0.219	**<0.0001**			
		StationBS	-0.726	0.232	**0.0020**			
		s(Year)				4.594	8.900	**<0.0001**
		s(TNN)				1.000	6.672	**0.0105**
Model 4	AIC = 639	Intercept	4.212	0.222	**<0.0001**			
	adj R^2 = 0.297	StationP4	-0.123	0.320	0.7000			
	Family = tweedie	StationM1	-0.185	0.283	0.5130			
		StationPM2	-0.140	0.297	0.6380			
		StationBS	0.097	0.301	0.7480			
		s(Year)				4.341	4.025	**0.0028**
		s(TP)				1.000	14.290	**0.0002**
		s(TNN)				1.000	5.058	**0.0256**
Model 6	AIC = 638	Intercept	4.047	0.218	**<0.0001**			
	adj R^2 = 0.254	StationP4	-0.052	0.313	0.8674			
	Family = tweedie	StationM1	-0.061	0.283	0.8301			
	p = 1	StationPM2	0.152	0.282	0.5905			
		StationBS	0.473	0.268	0.0792			
		s(Year)				4.179	4.479	**0.001**
		s(TP)				1.002	19.070	**<0.0001**

Table B7. Results of Dinophyta biovolume (mm^3/m^3) GAMMs from 1973-2016. Best model bolded. Significant p-values are bolded (p-value <0.05).

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth terms		
			estimate	Std. error	p-value	edf	F	p-value
Model 1	AIC = 677	Intercept	5.429	0.117	**<0.0001**			
	adj R^2 = 0.473	StationP4	-1.402	0.198	**<0.0001**			
	Family = tweedie	StationM1	-1.010	0.186	**<0.0001**			
		StationPM2	-1.219	0.192	**<0.0001**			
		StationBS	-0.984	0.185	**<0.0001**			
		s(Year)				12.570	14.570	**<0.0001**
Model 2	AIC = 671	Intercept	5.394	0.115	**<0.0001**			
	adj R^2 = 0.507	StationP4	-1.462	0.196	**<0.0001**			
	Family = tweedie	StationM1	-0.994	0.181	**<0.0001**			
		StationPM2	-1.140	0.189	**<0.0001**			
		StationBS	-0.872	0.187	**<0.0001**			
		s(Year)				12.760	13.598	**<0.0001**
		s(WT)				1.000	4.892	**0.0281**
Model 3	AIC = 620	Intercept	4.279	0.200	**<0.0001**			
	adj R^2 = 0.736	StationP4	0.164	0.310	0.5960			
	Family = tweedie	StationM1	0.338	0.248	0.1750			
		StationPM2	0.041	0.253	0.8710			
		StationBS	0.176	0.242	0.4680			
		s(Year)				16.384	7.988	**<0.0001**
		s(TP)				6.539	10.457	**<0.0001**
Model 4	AIC = 641	Intercept	5.492	0.106	**<0.0001**			
	adj R^2 = 0.570	StationP4	-0.959	0.190	**<0.0001**			
	Family = tweedie	StationM1	-0.920	0.167	**<0.0001**			
		StationPM2	-1.615	0.183	**<0.0001**			
		StationBS	-1.713	0.221	**<0.0001**			
		s(Year)				16.043	7.113	**<0.0001**
		s(TNN)				3.327	9.659	**<0.0001**
Model 5	AIC = 622	Intercept	4.296	0.201	**<0.0001**			
	adj R^2 = 0.746	StationP4	0.071	0.316	0.8220			
	Family = tweedie	StationM1	0.306	0.250	0.2220			
		StationPM2	0.054	0.254	0.8330			
		StationBS	0.216	0.243	0.3760			
		s(Year)				17.004	6.910	**<0.0001**
		s(TP)				6.104	10.150	**<0.0001**
		s(WT)				1.000	2.749	0.0990
Model 6	AIC = 613	Intercept	4.509	0.212	**<0.0001**			
	adj R^2 = 0.722	StationP4	0.004	0.310	0.9890			
	Family = tweedie	StationM1	0.135	0.254	0.5960			
		StationPM2	-0.300	0.279	0.2840			
		StationBS	-0.258	0.286	0.3670			
		s(Year)				15.843	6.712	**<0.0001**
		s(TP)				5.364	9.201	**<0.0001**
		s(TNN)				1.000	7.297	**0.0075**

Table B8. Results of Euglenophyta biovolume (mm^3/m^3) GAMMs from 1973-2016. Best model bolded. Significant p-values are bolded (p-value <0.05).

Model	Diagnostics	Terms	Parameter Coefficients			Significance of smooth terms		
			estimate	Std. error	p-value	edf	F	p-value
Model 1	AIC = 1603	Intercept	1.072	0.133	**<0.0001**			
	adj R^2 = 0.402	StationP4	-2.654	0.232	**<0.0001**			
	Family = tweedie	StationM1	-2.126	0.182	**<0.0001**			
		StationPM2	-1.538	0.142	**<0.0001**			
		StationBS	-0.598	0.100	**<0.0001**			
		s(Year)				34.420	15.540	**<0.0001**
Model 2	AIC = 1657	Intercept	1.004	0.136	**<0.0001**			
	adj R^2 = 0.822	StationP4	-3.210	0.265	**<0.0001**			
	Family = poisson	StationM1	-2.248	0.196	**<0.0001**			
		StationPM2	-1.576	0.162	**<0.0001**			
		StationBS	-0.834	0.150	**<0.0001**			
		s(Year)				32.450	11.580	**<0.0001**
		s(WT)				13.430	13.420	**<0.0001**
Model 3	AIC = 1526	Intercept	0.083	0.231	0.7212			
	adj R^2 = 0.699	StationP4	-2.010	0.372	**<0.0001**			
	Family = poisson	StationM1	-0.983	0.298	**0.0012**			
		StationPM2	-0.416	0.256	0.1053			
		StationBS	0.531	0.222	**0.0178**			
		s(Year)				34.811	11.000	**<0.0001**
		s(TP)				8.662	14.060	**<0.0001**
Model 4	AIC = 1680	Intercept	1.300	0.137	**<0.0001**			
	adj R^2 = 0.765	StationP4	-2.336	0.256	**<0.0001**			
	Family = poisson	StationM1	-2.013	0.191	**<0.0001**			
		StationPM2	-2.016	0.172	**<0.0001**			
		StationBS	-2.006	0.226	**<0.0001**			
		s(Year)				33.900	10.870	**<0.0001**
		s(TNN)						
Model 5	AIC = 1468	Intercept	0.489	0.215	**0.0245**			
	adj R^2 = 0.810	StationP4	-2.746	0.449	**<0.0001**			
	Family = poisson	StationM1	-1.353	0.295	**<0.0001**			
		StationPM2	-0.862	0.253	**0.0008**			
		StationBS	-0.003	0.223	0.9887			
		s(Year)				21.830	11.820	**<0.0001**
		s(TP)				11.540	8.642	**<0.0001**
		s(WT)				9.450	16.400	**<0.0001**
Model 6	AIC = 1577	Intercept	0.368	0.355	0.3014			
	adj R^2 = 0.846	StationP4	-2.289	0.481	**<0.0001**			
	Family = poisson	StationM1	-1.176	0.406	**0.0043**			
		StationPM2	-0.767	0.469	0.1040			
		StationBS	-0.053	0.523	0.9191			
		s(Year)				34.030	8.200	**<0.0001**
		s(TP)				12.803	10.088	**<0.0001**
		s(TNN)				4.589	3.882	**0.0025**