UPPSALA
UNIVERSITET

SLU

UPTEC W 24021
Examensarbete 30 hp
Juni 2024

Temperature-Induced Shifts in Size Spectra of Fish Communities in lakes

Olivia Åberg

Civilingenjörsprogrammet i miljö- och vattenteknik

UPPSALA
UNIVERSITET

SLU

Temperature-Induced Shifts in Size Spectra of Fish Communities in lakes

Olivia Åberg

Abstract

Climate change affects lakes, seas and running water globally, but the long-term effects on aquatic ecosystems, including fish communities, are complex and difficult to predict. Previous research has shown that changes in temperature, for example, can lead to shifts in fish species distribution and reductions in body size within fish communities. This study aims to investigate the impact of temperature on size distribution of individuals in fish communities by examining variations in so-called size spectrum and mean body size in ten Swedish lakes over the period 1994-2023. Data were collected from Swedish monitoring programs and analyzed using linear mixed-effects models. The result indicates a significant negative effect of temperature on the size spectrum and mean body size, meaning the number of small individuals increases while the number of large ones decreases. The size spectrum also shows a declining trend over time in several of the lakes, highlighting a shift in the size distribution of fish. These findings support the use of the size spectrum as an indicator of the impacts of climate change on freshwater ecosystems. The results of this study found a clearer link between temperature changes and size distribution compared to biomass, which supports the usefulness of size distribution as an indicator. Understanding these relationships is crucial for informing management and conservation strategies aimed at preserving lake ecosystems and the functions and ecosystem services that fish provide, including food and recreational opportunities. The study further contributes to the existing evidence that climate change is reshaping fish communities and aquatic ecosystems, underscoring the need for adaptive management to mitigate these effects and ensure sustainability of fish stocks for future generations.

Keywords: Climate change, Lakes, Aquatic ecosystem, Fish size distribution, Size spectrum, Linear mixed-effects model

Department of Aquatic Resources (SLU Aqua), Kustlaboratoriet, Almas allé, 750 07, Uppsala

Teknisk-naturvetenskapliga fakulteten

Uppsala universitet, Utgivningsort: Uppsala

Handledare: Magnus Huss & Benjamin Mooney Ämnesgranskare: Anna Gårdmark

Examinator: Fritjof Fagerlund

REFERAT

Temperaturinducerande förändringar i storleksspektra av fisksamhällen i sjöar

Olivia Åberg

Klimatförändringarna påverkar sjöar, hav och rinnande vatten globalt, men långsiktiga effekter på akvatiska ekosystem, inklusive fisksamhällens, är komplexa och svåra att förutse. Tidigare studier har visat att förändringar i temperatur till exempel kan leda till skiften i fiskarters utbredning och minskningar i kroppsstorlek i fisksamhällen. Denna studie syftar till att undersöka temperaturens inverkan på storleksfördelningen av individer i fisksamhällen genom att undersöka variation i det så kallade storleksspektrumets lutning och medelstorlek i tio svenska sjöar under perioden 1994–2023. Data samlades in från svenska övervakningsprogram för sjöar och analyserades med hjälp av linjära mixade effektmodeller. Resultaten indikerar en signifikant negativ effekt av temperatur på storleksspektrumets lutning och medelkroppsstorlek, dvs. antalet små individer ökar relativt antalet stora. Storlekspektrumets lutning visar också en nedåtgående trend över tid i flera av sjöarna, vilket belyser att fiskarnas storleksfördelning har skiftat mot relativt fler små individer i vissa sjöar. Dessa fynd styrker användningen av storleksspektrum som en indikator på klimatförändringarnas effekter på sötvattensekosystem. Resultat från denna studie visar också en tydligare koppling av förändrad temperatur på storleksfördelning än biomassor av fisk och växtplankton, vilket styrker nyttan av storleksfördelning som indikator. Att förstå dessa samband är avgörande för att vägleda förvaltnings- och bevarande strategier som syftar till att bevara sjöekosystem, de funktioner samt ekosystemtjänster som fiskar tillhandahåller, såsom mat och rekreationsmöjligheter. Studien bidrar till redan existerande bevis på att klimatförändringarna omformar fisksamhällen och akvatiska ekosystem, vilket tydliggör behovet av adaptiv förvaltning för att mildra dessa effekter och säkerställa starka fiskbestånd för framtida generationer.

Nyckelord: Klimatuppvärmning, Sjöar, Akvatiska ekosystem, Fiskstorleksfördelning, Storleksspektrum, Linjär blandade effekter modell

Institutionen för akvatiska resurser (SLU Aqua), Kustlaboratoriet, Almas allé 5, 750 07, Uppsala

PREFACE

This Degree Project, worth 30 credits, mark the end of my studies in the Environmental and Water Engineering program at Uppsala University and Swedish University of Agricultural Sciences. My primary supervisor was Magnus Huss, and my deputy supervisor was Benjamin Mooney, Department of Aquatic Resources (SLU Aqua), Swedish University of Agricultural Sciences. The subject reviewer was Anna Gårdmark, Department of Aquatic Resources (SLU Aqua), Swedish University of Agricultural Sciences.

Acknowledgments

I would like to say a big thank you to my two supervisors Magnus Huss and Benjamin Mooney, who have both been incredibly supportive and helpful during my master thesis work. Thank you for welcoming me with open arms and teaching me so much about the subject!

Olivia Åberg
Uppsala, June 2024

UPTEC W 24 24021, ISSN 1401–5765

POPULÄRVETENSKAPLIG SAMMANFATTNING

Varmare klimat gör att insjöfiskar i Sverige blir mindre

Denna studie tyder på att globala klimatförändringar kan komma att påverka ekosystemen i svenska sötvattensjöar negativt. Högre vattentemperatur leder bland annat till att medelfisken blir kortare och väger mindre. Människor drabbas i förlängningen av att de stora fiskarna blir färre – fisket blir sämre och en viktig tillgång på föda kan gå förlorat för framtida generationer. För att återställa balansen i ekosystemen och stärka sötvattensjöarnas motståndskraft krävs effektiva åtgärder mot klimatförändringarna och mer kunskap. Många konsekvenser är fortfarande oklara.

Det är som att bläddra i sidorna av en bok vars slut vi ännu inte vet. Klimatförändringar och mänsklig aktivitet utgör hot mot vår världs ekosystem, inklusive ekosystemen i sjöar, vars sårbarhet bli alltmer uppenbar för varje sida vi vänder på. Just nu förstärker klimatförändringar redan befintliga störningar i ekosystemen, och en av de mest drabbade organismgrupperna är fiskarna. Fiskarna, som utgör en viktig roll i balansen av livet i sjöar, är hårt pressade av klimatförändringen. De senaste 100 åren har vi bevittnat en ökning av jordens medeltemperatur, där vi under de senaste tio åren registrerat de varmaste temperaturerna någonsin. Vi ser idag inga indikationer på att temperaturökningen avtar. Uppvärmningen, en direkt följd av våra egna aktiviteter, resulterar i högre vattentemperaturer i många sjöar, vilket påverkar världen där små fiskar gynnas relativt de stora. Denna förändring i storleksfördelningen påverkar inte bara fisksamhällena utan i vissa fall även oss människor, genom att hota viktiga födokällor och ekonomiska verksamheter såsom fiske- och turistnäringarna. Dessutom kan det påverka våra fritidsaktiviteter.

Resultaten från denna studie visar att varmare temperatur har en negativ effekt på både medelstorleken hos fiskar och på fördelningen mellan fiskar av olika storlek i sjöar. Detta kan innebära att antalet små fiskar ökar relativt antalet stora fiskar. Resultatet i denna studie, har också visat sig vara oberoende av tillgång på näring (fosfor). Det i sin tur tyder på att temperaturförändringarna kan driva förändringar i storleksfördelningar av fisksamhällen i samma riktning i många olika typ av sjöar. Under perioden 1994 till 2023 observerades en betydande förändring i fördelningen av fisksamhällena i flera, men inte alla, av de studerade sjöarna. Skiftet mot relativt fler små än stora fiskar kan både vara en konsekvens av och resultera i en mindre effektiv energiöverföring från små individer till större individer på högre nivåer. Därigenom minskar tillgången på stora fiskar som fyller en viktigt ekologisk roll och som annars också skulle kunna fungera som en viktig tillgång på föda. Resultaten tyder också på att storleksfördelning kan vara ett sätt att i tid se signaler av yttre påverkansfaktorer, snarare än att endast följa antalet eller massan av fiskar.

Förståelsen av hur klimatförändringar påverkar fisksamhällen och vattenekosystem är av avgörande betydelse. Det är därför viktigt att till exempel fortsätta övervaka hur fiskstorleken i sjöar påverkas av varmare temperaturer för att säkerställa långsiktigt starka fisksamhällen och ekosystemfunktioner. Fiskarna och ekosystem i sjöar är inte bara viktiga för att bevara biologisk mångfald och naturliga resurser, utan också för att tillhandahålla livsmedel, bidra till vattenrening och reglera klimatet. Genom att aktivt hantera och mildra effekterna av klimatförändringar på dessa ekosystem kan vi förbättra vår förmåga att förutse förändringar och anpassa vår förvaltning av ekosystemen. Det skulle inte bara gynna nuvarande generationer utan även ge bättre förutsättningar för framtida generationer att dra nytta av sjöarnas resurser. Dessutom, genom att förstå samspelet mellan fiskar, ekosystem och människor kan vi bättre utveckla mer effektiva åtgärder och hållbara förvaltningsstrategier. Detta är avgörande för att bevara och stärka sjöekosystemens motståndskraft mot klimatförändringar och annan mänsklig påverkan.

En ökad förståelse för hur temperatur och andra miljöfaktorer påverkar storleksfördelningar av fisk kan hjälpa oss att upptäcka påverkan av mänskliga aktiviteter och förutse framtiden med bättre precision. Vi kan välja hur vi vill forma slutet av denna historia genom att anstränga oss och använda den kunskap vi besitter för att bevara fisksamhällena och balansen i ekosystemen. Det skulle hjälpa att skriva om slutet i denna bok och se till att det blir ett lyckligt slut för alla inblandade – både människor och fiskar.

WORDLIST

Term	Definition
Anthropogenic impact	Effects on nature caused by human impact (Nationalencyklopedin n.d.)
CPUE	Abbreviation for catch per unit effort. It measures the amount (number or biomass) of fish caught per standard unit of fishing effort, in this case per net areas and night (Cochrane 2002.).
Fish community	All individuals, including all species, of fish living and interacting together in a specific habitat or area, e.g. a lake (HELCOM n.d.).
Fish population	All the individuals of the same fish species living in a specific habitat or area, e.g. a lake (HELCOM n.d.)
Food web	Food webs are a vital tool that illustrates feeding relationships among organisms and species, revealing interactions, community structure and energy dynamics in an ecosystem (Hui 2012).
Size spectra	Size spectra refer to how biomass is distributed across different body size classes within an ecological community (Benoît & Rochet 2003).
Trophic levels	Organisms in a food web are divided into trophic levels based on their feeding behavior and position in food chain. The levels include producers like phytoplankton, herbivores (plant eaters) such as zooplankton and carnivores (meat eaters) such as fish (Britannica 2023).
Trophic transfer efficiency	Calculated as the amount of energy transferred between two consecutive trophic levels, ideally as the ratio of production rates between trophic levels (Mehner et al. 2022).

TABLE OF CONTENTS

1. INTRODUCTION

Many of the ecosystems on Earth, including freshwater ecosystems, are threatened by human activities, which can affect both physical, chemical, and biological components (Bouraï et al. 2020). Climate change is now adding to other human pressures potentially leading to disturbances in ecosystems. One example of an organism group that is affected by climate change is fish, which play a crucial role in aquatic ecosystems and are a vital food source for both top predators and humans (Holmlund & Hammer 1999; Jeppesen et al. 2012). The population sizes of many fish populations around the globe are decreasing because of human activities, which may threaten numerous vital ecosystem services provided by fish, such as nutrient cycling and food provisioning (Canosa & Bertucci 2023). Aquatic predators, such as fish, play a crucial role in maintaining ecosystem functions and services, both directly and indirectly (Hammerschlag et al. 2019). Therefore, losses of predators such as large fish may also lead to the loss of ecosystem functions. Additionally, previous research suggests that higher trophic levels, containing heterotrophic organisms (e.g. fish), are more sensitive to warming than the autotrophs (e.g. phytoplankton) (Dolbeth et al. 2012). This difference in sensitivity can lead to increased consumption relative to primary production, potentially altering top-down control and the relative biomass of consumers relative to primary producers in warm relative to cold waters (Dolbeth et al. 2012; Nagelkerken et al. 2020). Another example of how fish communities respond to climate warming is by reduced body sizes in warmer temperatures, driven by for example high population turnover rate and increased reproduction rate (Baudron et al. 2013; Arranz et al. 2021). Aquatic predators can provide benefits to humans, so a reduction in their numbers and size can affect fisheries, food, and tourism (Hammerschlag et al. 2019). This reduction can potentially lead to negative economic consequences due to the loss of ecosystem services provided by fish populations. Even if fish populations often adapt to specific environmental conditions, which is crucial to maintain resilience and functionality, fish communities should not be allowed to decline today under the assumption that they will naturally recover later (Holmlund & Hammer 1999). For example, conserving in nature reserves alone may not be sufficient for compensation.

It is of great importance to admit the relationship between fish populations and human societies especially in the context of climate change (Hammerschlag et al. 2019). Additionally, fishes serve as indicators of the ecosystem health and stress levels. Moreover, in addition to longstanding threats like overfishing and eutrophication, fish is now facing additional threat of global warming (Nagelkerken et al. 2020), compromising the stability and dynamics of both fish and aquatic ecosystems (Arranz et al. 2023), along with their functions (Bouraï et al. 2020).

Since 1900, the average temperature on Earth has increased with 1 degree Celsius with the ten warmest years recorded in the last decade (National Oceanic and Atmospheric Administration (NOAA) 2024). As a result of warmer temperatures due to climate change, many lakes in Europe have experienced an increase in water temperature (Jeppesen et al. 2012). This has, for example, resulted in changes in the composition of fish communities and mean body size of fish communities (Arranz et al. 2023).

1.1 TEMPERATURE EFFECTS ON FISH BODY SIZE

Climate change does not only affect the size of populations and communities but also body size distribution of aquatic organisms (Arranz et al. 2023). Such changes can in turn influence both ecological and evolutionary processes as well as population dynamics, community stability and ecosystem functioning. Several studies suggest that warming leads to decreased mean body size of fish populations, and thus also changes in the distribution of body sizes within communities (Baudron et al. 2013; Boltaña et al. 2017; Arranz et al. 2023). Warmer water has been shown to benefit small-bodied individuals more than larger individuals, leading to shifts in body size distribution and changes the composition between small and large individuals within communities (Baudron et al. 2013; Bouraï et al. 2020; Arranz et al. 2023). The decline in adult body size with temperature is known as the temperature size rule (Atkinson et al. 1994 see Baudron et al. 2013; Arranz et al. 2023). One, out of several different ones, potential explanation is that warmer temperatures decrease body size in fish populations primarily due to the smaller individuals' ability to cope better with oxygen deficiency than larger individuals (Baudron et al. 2013). This deficiency is caused by decreased aerobic capacity at higher temperatures. Another general reason why warmer temperatures can change organisms' sizes, is because different temperatures affect the metabolic rate (Gillooly et al. 2001; Norkko et al. 2013). Metabolic rates, in turn, affect biomass production (Reiss et al. 2009).

Fish are not only affected by direct and indirect effects of temperature change, but also concurrent change in extent of nutrient concentrations, stratification (Jeppesen et al. 2012) and species interaction (Boltaña et al. 2017). For example, Bouraï et al. (2020) found in their study that mean body size decreased when temperature increased, and when the levels of nutrients were low. Similarly, if the lake experiences excess phosphorus, it can negatively impact growth rate (Benstead et al. 2014). Excess phosphorus in waters can affect light availability by eutrophication symptoms such as rapid algal growth and cause oxygen limitation and hypoxia (Nathanailides et al. 2023). These conditions can favor smaller individuals, as they often adapt better to low-oxygen environments and can exploit the available food. Also, a warm lake can be more sensitive than a cold to increased phosphorus concentrations in terms of lack of oxygen, which can lead to dead fish and increased biological activity such as algal growth (Witek-Krowiak et al. 2022). Nevertheless, it has been pointed out that depending on the physical characteristics of different lakes, they react differently to climate change and changes in phosphorus levels, also suggesting that lakes are more or less vulnerable to having human operations such as agriculture or forestry near them (Malmaeus et al. 2006). Phosphorus is typically the primary limiting nutrient during most of year for primary production in many freshwater ecosystems (Ahlkrona 2002; Malmaeus et al. 2006). Even if other nutrients also can limit primary production (e.g. Elser et al. 2009), the amount of phosphorus needed is smaller and recycled faster than nitrogen and silicon (Ahlkrona 2002). Human activities such as agriculture with synthetic fertilizers and wastewater runoff contribute to releasing phosphorus into freshwater ecosystems (Witek-Krowiak et al. 2022).

Today there are relatively few studies that have looked at the combined effects of nutrient enrichment and temperature on aquatic organisms in freshwater ecosystems (Rodgers 2021). The above-mentioned effects of climate warming on the number and size of individuals can, in turn, decrease biomass production in fish populations and communities (Gårdmark & Huss 2020). It may also affect the efficiency of energy conversion and transfer in the ecosystem and thus change the distribution of biomasses and affect interactions between different species, such as predator-prey, competition, and other ecological interactions (Mehner et al.

2022). Such shifts in interactions can also reduce trophic transfer efficiency, which is the ratio of production rates of two successive trophic levels. Reduced trophic transfer efficiency can, for example, lead to decreased growth rates and abundance of consumers, especially at higher levels. This is because the energy transferred between trophic levels is reduced, meaning that less energy is available for consumer growth, and abundance therefore decreases because there may not be enough energy to support the larger individuals, often predators (Mehner et al. 2022).

Arranz et al. (2023) points out that we need to do more empirical research about how climate warming shape wild communities to gain better insights into how human pressures is affecting body size. This includes studying how warmer temperatures contribute to decreasing body size, while also consider the interactive effects of factors such as land use and exploitation. The effects from climate warming should thus not be taken into consideration alone, but together with other human pressures on freshwater ecosystems that could make the warming effects on these ecosystems more or less negative (Bouraï et al. 2020; Nagelkerken et al. 2020). However, it is largely unexplored how a warming climate and other human pressures combined is affecting body size distributions (Arranz et al. 2021; Arranz et al. 2023).

1.2 COMMUNITY SIZE SPECTRUM

In aquatic ecosystems, one of the most important ecological traits is body size due to its important role in determining ecological rates and interactions between organisms and due to its responsiveness to environmental conditions (Marin et al. 2023). The relationship between body size and abundance of individuals in communities, referred to as the community size spectra, can provide insights into ecosystem health. It provides insight because the distribution of organisms within a community can indicate environmental stress and ecosystem function, and specifically inform about the flow of energy through trophic levels (Andersen et al. 2016). Size spectra thus reflect trophic interactions and trophic transfer efficiency from lower to higher trophic levels, highlighting the importance of body size in shaping ecosystem functions (Atkinson et al. 2024). Additionally, the temperature-size rule suggests that warmer temperatures influence the size spectrum slope by decreasing adult body size (Aguilar-Alberola & Mesquita-Joanes 2014). Size spectra can also help infer human pressures such as overfishing, pollution and habitat destruction by identifying changes in size distribution of fish resulting from these activities. Furthermore, size spectra can provide valuable insights into how fish communities respond to warmer climates and therefore work as indicators of environmental changes (Arranz et al. 2023).

Continuing on the important role of size spectra in understanding aquatic ecosystems and their use as an indicator can reveal the consequences of human impacts (Petchey & Belgrano 2010). An indicator that responds to human activities can help with environmental monitoring and can provide insights into ecosystem status. Size spectra is one such indicator that can be used to assess not only the effects of climate change but also selective fishing and habitat exploitation (Benoît & Rochet 2003; Shin et al. 2005). As Marin et al. (2023) states, using size spectra as indicator can help quantify deteriorated water quality affected by agriculture, forestry, and domestic effluents, thereby highlighting threats to lake ecosystems.

While the effects of human pressures on the fish size spectrum in marine ecosystems are relatively well studied, impacts on freshwater ecosystems remain less studied, including in relation to climate change (Edwards et al 2017; Arranz et al. 2021). Variation in size spectrum slopes, often based on grouping fish into size classes, can reveal both the impact of exploitation and variation in the flux of energy through food webs (Mehner et al. 2022; Atkinson et al. 2024). Also, size spectrum theory relates to a broader time-spatial scale than those typically analyzed in studies, which often focus on individual systems or individual observation from various systems (Atkinson et al. 2024). Often, the size spectrum is calculated using bins of individual body size on a logarithmic scale (log2-scale) (Arranz et al. 2021; Atkinson et al. 2024, see Figure 2 for an example of how it can appear). Alternative ways to calculate size spectrum is by using maximum likelihood estimates, normalized logarithmic binning, log-transforming data plus 1 or plotting the logarithm of 1 minus the cumulative distribution etc. (Edwards et al. 2016). The slope of the size spectrum reflects the linear rate of decline in fish biomass with increasing body size. A more negative value of the slope suggests lower efficiency in energy transfer, with smaller individuals within a community constituting a larger proportion of the total biomass compared to larger individuals (Norkko et al. 2013; Arranz et al. 2021; van Dorst et al. 2022). Recent studies suggest that the actual value of size spectrum slope often varies in response to environmental, anthropogenic, and biotic factors (Marin et al. 2023; Canosa & Bertucci 2023). Given such variation, the value of size spectrum can give a quantifiable and comparable index to e.g. infer environmental impacts on ecosystems (Arranz et al. 2021). It also offers another perspective on energy transfer efficiency along food webs compared to production or biomass ratios of different trophic levels (Atkinson et al. 2024).

With all projections suggesting continued climate warming (NOAA 2024), in combination with an expanding human population on Earth, there is also the risk of additional environmental stressors to worsen such as increased nutrient (phosphorus) loading to lakes and sea areas. Increasing phosphorus concentrations can become an issue because of more agricultural activities and wastewater with an increase in population size (Nathanailides et al. 2023). Studies conducted in lakes in the Western Palearctic have shown that warmer temperature and higher nutrient concentrations predominantly benefits smaller body sizes of fishes and leading to a reduction in the number of larger fish and thus a decrease in the size spectrum slope (Arranz et al. 2021). In Northern Europe, we witness both rising and falling trends in nutrient concentrations in our lakes (Huser et al. 2018). Despite this variability, lakes have a natural pattern of seasonal changes in nutrient levels, and it seems that climate change is intensifying this natural pattern (Yindong et al. 2021). However, the responses of changes in nutrient availability under warming remains unclear. This highlights the need for additional research on the impact of climate warming on nutrients dynamics, and what implications it has on aquatic ecosystems.

1.3 AIM OF THE STUDY

Understanding how fish body size and size spectrum slopes are influenced by higher temperatures and other human pressures is of great importance because it could inform us about changes in ecosystem functions and services (Bouraï et al. 2020), and thereby help us undertake mitigation actions. The reality of global warming and its effects on aquatic ecosystems underscores the urgency of this research, especially given human reliance on fish for food, income, and recreation. Here, especially the extent to which warming affects energy transfer up the food chain and thus biomass production of fish is of key importance. This study aims to investigate (i) the effects of temperature on fish size distribution by means of size spectrum slopes over time in lakes, (ii) if those effects vary depending on nutrient availability and (iii) if the fish size spectra and the ratio of fish to phytoplankton biomass, as alternative measures of trophic transfer efficiency, show similar responses to variation in temperature. To achieve this, the fish community size spectrum slopes are determined using data covering a period of 29 years from ten Swedish lakes, including biomass data for both fish and phytoplankton.

This research aims to answer the following question:

Do, and if so, how much do fish community size spectrum slopes change with temperature in Swedish lakes?

I hypothesize that small-bodied fish will increase in biomass in response to warmer temperatures relative to larger individuals, leading to steeper size spectrum slopes and decreased mean body size over time, as they may benefit more from warmer temperatures. I also hypothesize that higher amounts of total phosphorus benefit smaller individuals, resulting in the size spectrum slope decreasing.

2. METHOD

Below the data used and how they were retrieved, selected, and analyzed is described.

2.1 STUDY LAKES

The study lakes include 10 so called trend lakes (Figure 1), that are part of the Freshwater monitoring program of the Swedish Agency for Marine and Water Management (Swedish University of Agricultural Sciences (SLU) 2023). The aim with the Freshwater program and trend lakes is to evaluate large-scale impact and assess environmental quality on lake ecosystems from a national perspective, by measure lake water chemistry and biology (Havs- och vattenmyndigheten 2014). The 10 lakes were selected based on the following criteria: (1) The monitoring of the lakes with respect to chemistry and phytoplankton has been done several times throughout a year (Fölster et al. 2014; SLU 2023). (2) The lakes needed to have both fish (sampled at least once per year), phytoplankton, and water chemistry data for the years 1994 to 2023, specifically for the months June-August. This selection was done to be able to compare fish data with environmental data. The years 1994 to 2023 was chosen because data was available for each year, month and lake needed.

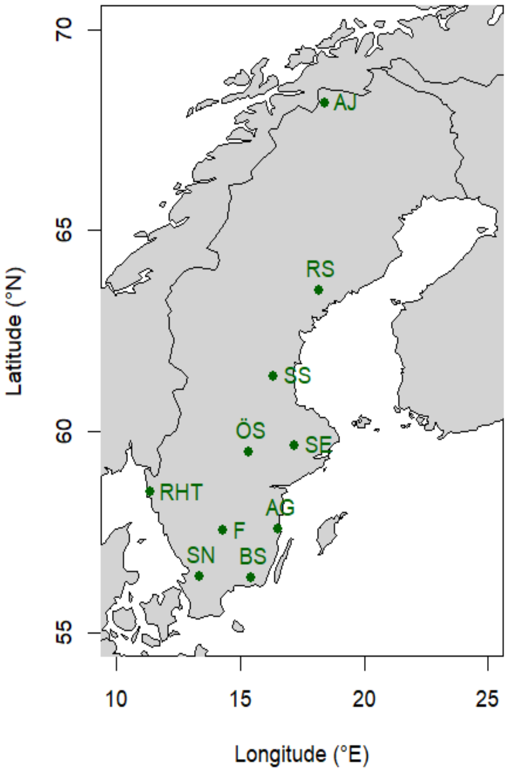

Figure 1: Selected study lakes with abbreviations. AJ stands for Abiskojaure, RS for Remmarsjön, SS for Stensjön, ÖS for Övre Skärsjön, SE for Stora Envättern, RHT for Rotehogstjärnen, AG for Allgjutten, F for Fiolen, SN for Stora Skärsjön and BS for Brunnsjön (for details, see Table A1 in Appendix).

2.2 ENVIRONMENTAL VARIABLES

The environmental parameters were obtained, including water geochemistry and phytoplankton, from the Miljödata-MVM (2024-02-02) database. The environmental variables, used as explanatory variables, are water temperature and total phosphorus, but in addition biovolume of phytoplankton (mm^3 / l) is also used, which is available in the same database, as one of the response variables. Water temperature and total phosphorus are sampled every month during the summer months each year for each lake, whereas phytoplankton biovolume is sampled 4 times per year, including at least one measurement in July or August.

In this study, data is included only for the main growth season, and therefore using mean values for samples collecting June to August for the years 1994 to 2023. The reason for choosing this specific time-period (June-August) was to ensure that only the ice-free season was included (also for the lakes located more north) and to capture the peak of summer water temperatures when production and growth rates of most organism are high (Canosa & Bertucci 2023). Furthermore, this time-period is relevant when comparing the environmental data to the fish data, as fish are only sampled in July and August.

2.2.1 Sampling of environmental data

The collected environmental samples were analyzed by the laboratories at the Aquatic Sciences and Assessment department, certified by SWEDAC – Swedish Board for Accreditation and Conformity (Fölster et al. 2014).

Water geochemical data were selected and obtained from water samples taken at 0.5 depth with a tube sampler of the type Ruttner and taken in the middle of each lake (Fölster & Stensdotter Blomberg 2016). The samples were kept cool when transported back to laboratory and all analyses for water chemistry characteristics followed international (ISO) or European (EN) standards: SS-EN ISO 5667-1:2007, SS-EN ISO 5667:3-2004, ISO 5667-4 (Fölster & Stensdotter Blomberg 2016).

The phytoplankton data was obtained by using a 2-meter-long tube sampler in the middle part of each lake (Drakare 2021). After sampling, the water samples with phytoplankton were preserved with iodine-potassium iodide. The species composition and biomass of phytoplankton was determined using an inverted microscope and the Utermöhl (1958) technique (for details, see Drakare 2021).

2.2.2 Derivation of temperature

The key explanatory variable in the analyses of this study is temperature, which, similar to the chemical data, was sampled monthly in the study lakes. A limitation of using water temperature in this case is thus the low frequency of collected water temperature, which is also why air temperature is used. Air temperature was retrieved for each lake coordinates from the SMHI model PTHBV – Precipitation Temperature Hydrologiska Byråns Vattenmodell (2024). The model is designed for hydrological calculations and includes daily estimates of temperature and precipitation values (SMHI 2024). After retrieving the air temperature data, correlations between air temperature and water temperature for each lake were tested (SMHI 2024). A significant correlation between air and water temperature was found for all lakes ($p\text{-value} < 2.2e\text{-}16$, $R^2 = 0.87$). Air temperature is therefore chosen in the analyses because this gives more continuous estimates and therefore allow for better estimates of growth season means.

Additionally, lagged temperature is included in the statistical models with fish data, because of the expected time lag in the effect of temperature on fish communities. The lagged temperature was calculated by taking a mean of the three previous years, giving a time-period of lagged temperatures on years 1997 to 2023. This was not done for analyses with phytoplankton, which have much shorter generation times and thus faster responses to environmental change.

2.3 FISH DATA

The fish data used were obtained from the Swedish National Register of Survey test-fishing (NORS 2024). These data included year, species, length per individual (mm), depth, weight (g), net code and if the net were in the pelagic or benthic zone. Fish are sampled each year during the summer, in July or August. The 10 lakes sampled 1994-2023 together included 186 563 individuals of fish and 17 different species. The species undefined carp-fish is included in common carp.

2.3.1 Sampling of fish

The sampling of fish is done by a standardized method of fish sampling in lakes, using multimesh benthic and pelagic gillnets (FINFO 2001) with the aim to get representative data of species presence, numbers, and size distributions according to SS-EN 14757:2015 (Swedish institute for standards 2015). The method is developed for monitoring programs, i.e. the Freshwater program, to detect changes in the development of lake fish communities, both within lakes over time and to compare different lakes. Pelagic nets (length 27,5m, height 6m with 14 sections with mesh sizes between 6.25-75 mm) are placed in the open free water zone. Bottom-standing benthic nets (length 30m, height 1,5m, with 12 sections with mesh sizes between 5-55 mm) are placed in different depth strata to capture the whole fish community for a lake, and the number of nets is standardized to the size and maximum depth of each lake (Appelberg 2000). Even if the aim is to capture the whole fish community, it is important to note that the smallest fishes may not be captured because of mesh sizes being too big for the smallest ones (e.g. most of the young-of-the-year fish). The nets are placed in the lake before dusk and picked up after dawn such that the nets will be in the lake for around 12 hours. The net time should include the period when the fishes are the most active. Captured fish are measured to the nearest millimeter and identified to species (FINFO 2001).

Fish catches are summarized as the variable CPUE, catch per unit effort for both benthic and pelagic nets. For calculating the ratio between fish CPUE and phytoplankton biovolume later, both is converted to carbon mass, see equation 1 (Blomqvist et al. 1994) and 2 (Czamanski et al. 2011). Most fish were caught in benthic nets (79%), leading to analyzing fish caught in these nets in this report.

$$Total\ Biovolume_{carbon\ mass} = \frac{Chlorophyta\ \left(\frac{mm3}{l}\right)}{1000} \times 0.16 + \frac{Cyanobacteria\ \left(\frac{mm3}{l}\right)}{1000} \times 0.22 + \frac{Other\ phytoplankton\ \left(\frac{mm3}{l}\right)}{1000} \times 0.11 \tag{1}$$

$$CPUE_{carbon\ mass} = \frac{CPUE\ biomass\ (\frac{g}{m^2})}{10} \tag{2}$$

2.3.2 Fish community size spectrum

In addition to the mean length of the fish communities for each year and lake, size spectrum slopes are calculated based on individual weights to study fish size distributions across lakes and as a function of environmental variables. To calculate size spectrum slopes, the estimated weights for each individual fish are first determined. This was done using length-weight relationships (Eqn 3), with parameter values from FishBase (Froese & Pauly 2022), specific for each species in the catch (see Table A2 in Appendix for species-specific coefficients).

$$W = a * L^b \tag{3}$$

The variable a represents a species-specific scaling coefficient for the species weight relative to the length and b a shape parameter which describe the specific body form (Kuriakose 2017). Because the net catches do not represent the smallest and largest individuals accurately (FINFO 2001), this study only included individuals larger than 6 cm and with the corresponding weights ranging from 8 to 2000 grams for the calculation of size spectrum slopes (similar to e.g. van Dorst et al. 2022).

After calculating individual weights these were divided into bins with log2-transformed constant width (Edwards et al. 2017). To standardize data among lakes and years, the number of bins were fixed to 8, resulting in the same size classes (bins) for each lake (8-16, 16-32, 32-64, 64-128, 128-256, 256-512, 512-1024, 1024-2048). See Figure 2 for an example for lake Abiskojaure and how the bins may appear for a lake.

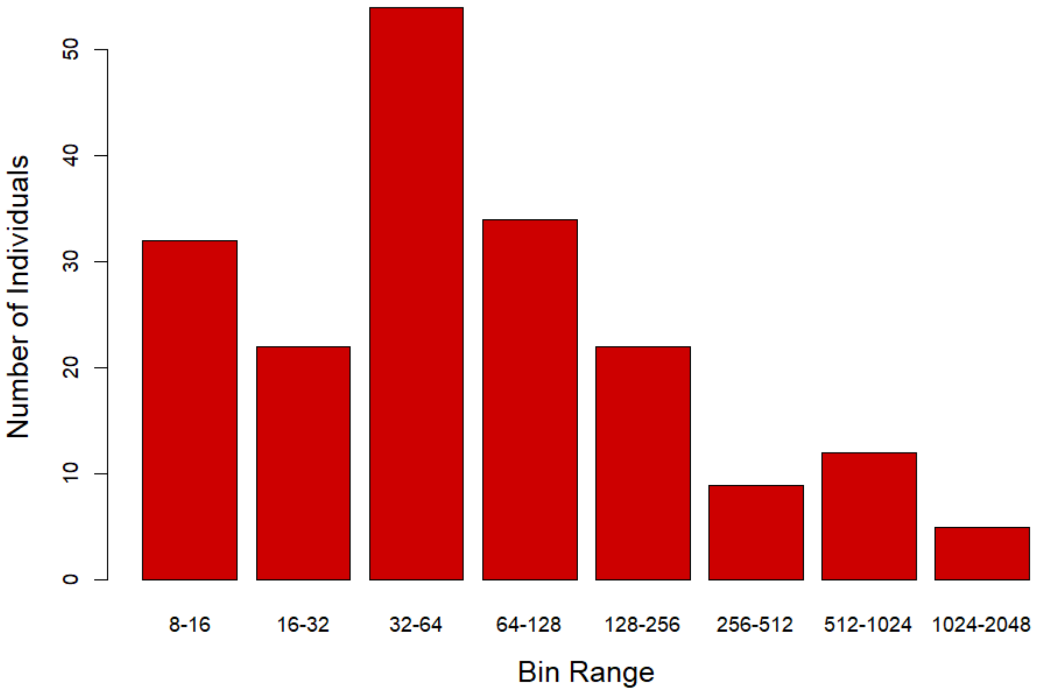

Figure 2: Bin representation of the coldest lake among the trend lakes (Abiskojaure), visualizing how it looks when binning the data. This is only for year 2023.

Then, to estimate the size spectrum slope for each lake-year, linear regressions (See example for one lake and year in Figure 3) were done based on the number of individuals per size class, using log-transformed mid-point values for each size class (Edwards et al. 2017). The size spectrum slope (b) was calculated for each year for each of the 10 trend lakes, with the slope of the size spectrum indicating the rate by which the abundance of individuals decreases with body size (Arranz et al. 2023).

The total number of fish used to calculate mean size and size spectrum slopes, based on the specified criteria, was 180 834.

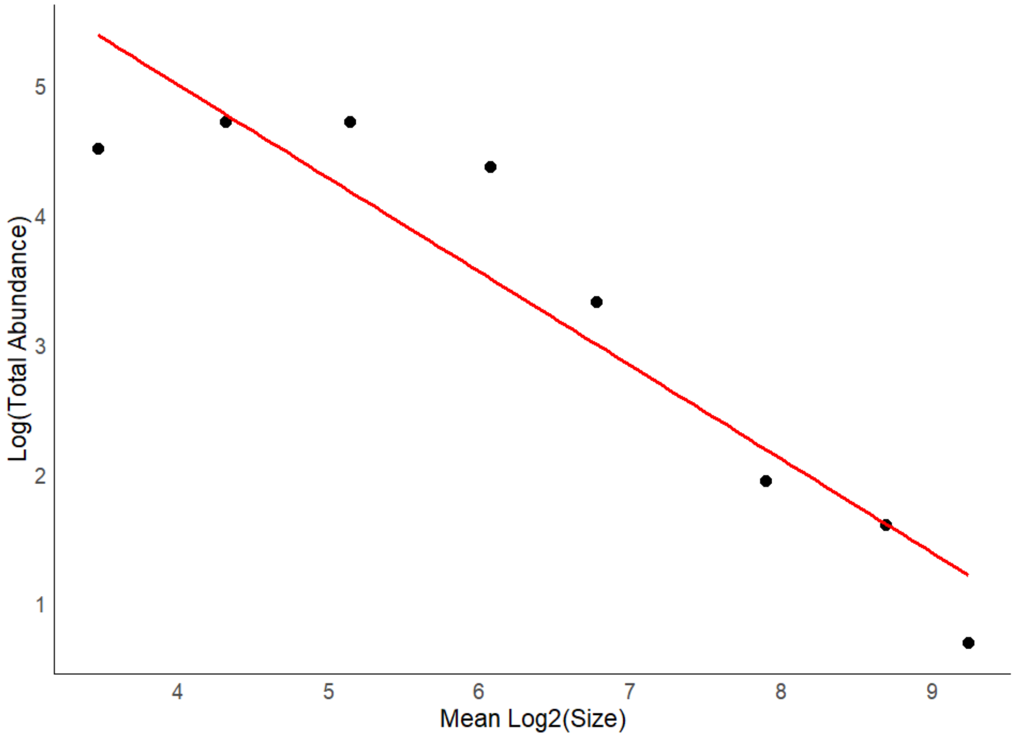

Figure 3: Regression line used to derive the size spectrum slope (b), exemplified for lake Abiskojaure, year 2023.

2.4 STATISTICAL ANALYSIS

To test the hypothesis if the response variables, mean fish body size, the proportion of large relative to small fish (size spectrum slope), biovolume of phytoplankton, catch per unit effort of fish caught with benthic gill nets (CPUE B) and the ratio of fish to phytoplankton biomass decrease with temperature, controlling for the potential effect of nutrient availability (i.e. covariate), a linear mixed-effects model is used. Both mean body size and size spectrum slope is looked at because mean body size provides a measure of the average size of individuals within a community. Meanwhile, size spectrum slopes indicate the relationship between fish abundance and body size and can shed light on energy transfer dynamics. Phosphorus is included as a covariate to account for variability in the response variable that is not explained by the primary explanatory variable, in this case temperature. This helps to isolate the effect of the primary explanatory variable, providing a clearer and more accurate understanding of its impact.

The models were constructed using the *nlme* package in R, using the *lme* function. Initially, a response variable is specified, followed by the order of explanatory variables under consideration, in this case mean growth air temperature and total phosphorus. Subsequently, random effects are determined. An example illustrating the structure of the model is provided in Appendix 2. Lake is included as a random effect such that the intercepts can vary randomly between all lakes, considering variation among lakes not accounted for by explanatory variables. Year is nested within lake, allowing for the effect of year to vary among lakes.

Mean length, biovolume of phytoplankton, CPUE B and the ratio CPUE B / phytoplankton were log-transformed to normalize data prior to analyses. Multicollinearity is tested for the explanatory variable and covariate with the variance inflation factor (VIF) from the package *car*. Multicollinearity is an important consideration in statistical analysis, as it directly affects the reliability and interpretability of results. For example, high multicollinearity indicated by a variance inflation factor bigger than 5 can impede the accurate interpretation of individual explanatory variables and result in less reliable estimates. Critical multicollinearity is found between total phosphorus concentration and the interaction term phosphorus × temperature (VIF>10), but in no case between temperature (main explanatory factor) and phosphorus (covariate). Normality of model residuals was evaluated with the Shapiro test and by visual inspection of residual plots (Figure A1-A5 in Appendix). This is done because of the importance to ensure that the differences between observed and predicted values follow a normal distribution, which is essential for reliable statistical inference (Helsel et al. 2020). Additionally, homoscedasticity, or the constancy of the variance of residuals across different levels of the independent variables, was examined through visual inspection of residual plots. It is important to ensure that the variability of residuals remains consistent across the range of predictor values to assure the validity of regression analysis results. Outliers were determined by checking if the absolute value for each point was greater than three times the standard deviation of the residuals. Outliers were removed before analyzes for each model to minimize their potential influence on distorting the results. 4 outliers were removed for the model with size spectrum slope, 0 for mean body size, 3 for the phytoplankton biomass and 2 for both the CPUE B and the ratio between CPUE B and phytoplankton models. Marginal and conditional R^2-values was calculated for all the mixed-effect models with the *r.squaredGLMM* function from package *nlme* to see how the extent to which fixed effects explain the variation (marginal) and the overall variability (conditional). All statistical analyzes in this report was done in RStudio 2023.12.1 (Build 402) (Appendix 2).

3. RESULTS

The size spectrum slope decreases with -0.044 per unit increase in temperature i.e. there was a negative effect of mean growth season temperature (hereafter temperature) on mean size (Figure 4) and size spectrum slopes (Figure 5) and thus the relative proportions of large relative to small fish individuals (Table 1). This was true irrespective of phosphorus concentration, and there was no interaction between temperature and total phosphorus (Table 1, and in Table 2 for the marginal and conditional R^2-values).

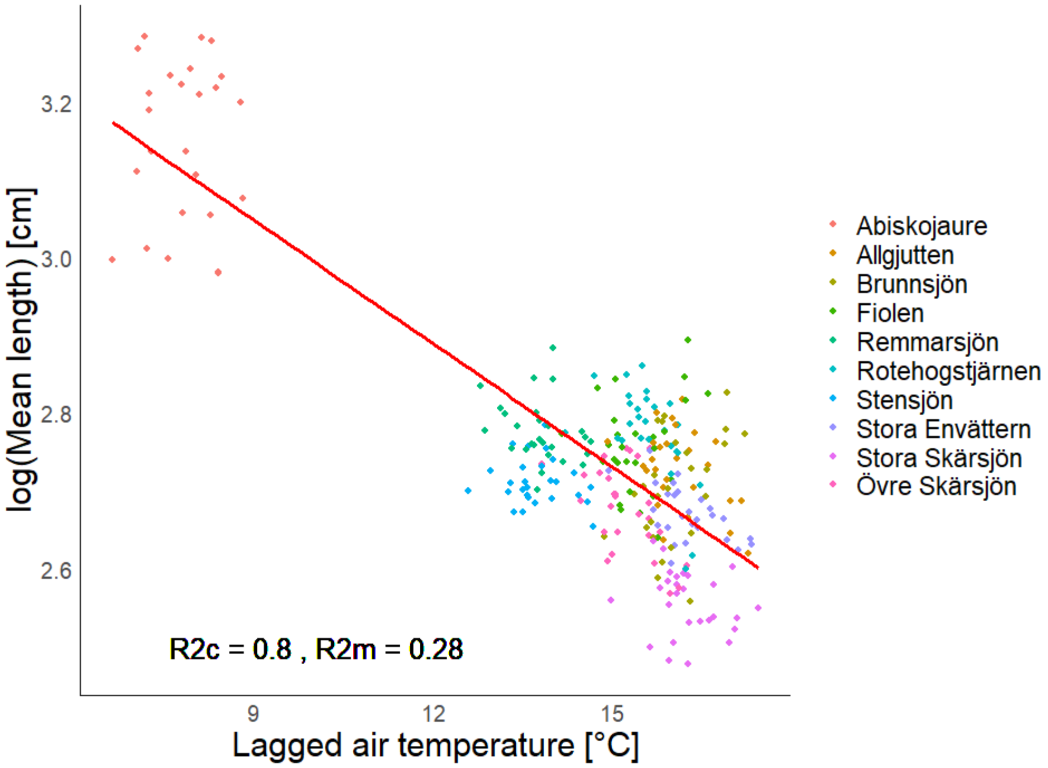

Figure 4: Mean size as a function of air temperature (June-August) for the studied lakes. The line represents predictions from the model: lme [log mean size ~ water temperature + total phosphorus+ water temperature:total phosphorus, random = ~ 1 + year | lake). Lagged air temperature refers to mean temperature for the previous three years. Each point corresponds to a value representing a specific year per lake. R2c stands for conditional R2-value and R2m for marginal.

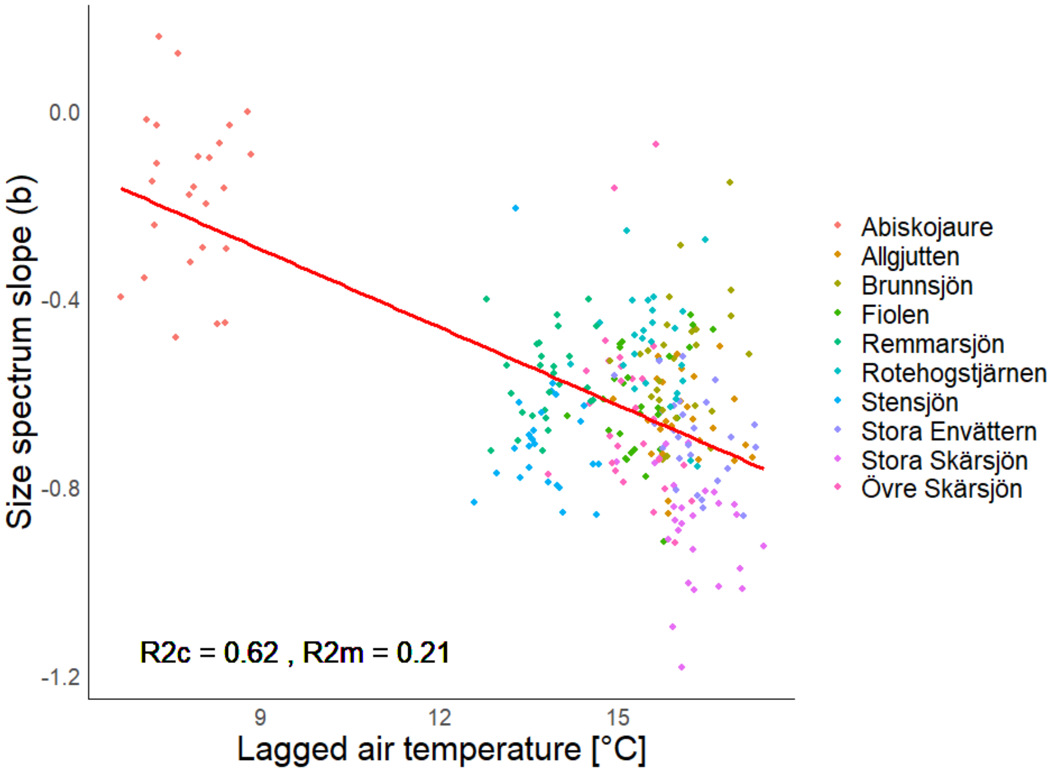

Figure 5: Size spectrum slopes as a function of air temperature (June-August) for the studied lakes. The line represents predictions from the model: lme [size spectrum slope ~ water temperature + total phosphorus+ water

temperature:total phosphorus, random = ~ 1 + year | lake). Lagged air temperature refers to mean temperature for the previous three years. Each point corresponds to a value representing a specific year per lake. R2c stands for conditional R2-value and R2m for marginal.

Table 1: Results of the mixed-effect model analyses on the effects on fish community size spectrum slopes (b) and mean body size in length, with t-values (used to assess the significance of the explanatory variable) and p-value, where a p-value smaller than 0.05 is indicating significance. Parameter estimates for both the models indicating the size of the effect of each explanatory variable are also presented.

	Size spectrum slope (b) t-value	**Size spectrum slope (b) p-value**	**Size spectrum slope (b) Parameter estimate**	**Mean body size t-value**	**Mean body size p-value**	**Mean body size Parameter estimate**
Air temperature	-2.33	0.02	-0.044	-3.03	0.003	-0.034
Total phosphorus	-0.38	0.71	-0.100	-0.97	0.33	-0.014
Temperature: total phosphorus	0.60	0.55	0.0010	1.01	0.31	0.0010

Table 2: Marginal (R^2 marg.) and conditional (R^2 cond.) coefficient of determination provided for models with the size spectrum slope and mean body size.

	Size spectrum slope (b)	**Mean body size**
R^2 marg.	0.21	0.28
R^2 cond.	0.62	0.80

The result indicates that there is minor effect of temperature, phosphorus or their interaction on phytoplankton carbon mass, fish catch per unit effort (CPUE) or the ratio between the two (Table 3; Figure 6). See Table 4 for marginal and conditional R^2-values.

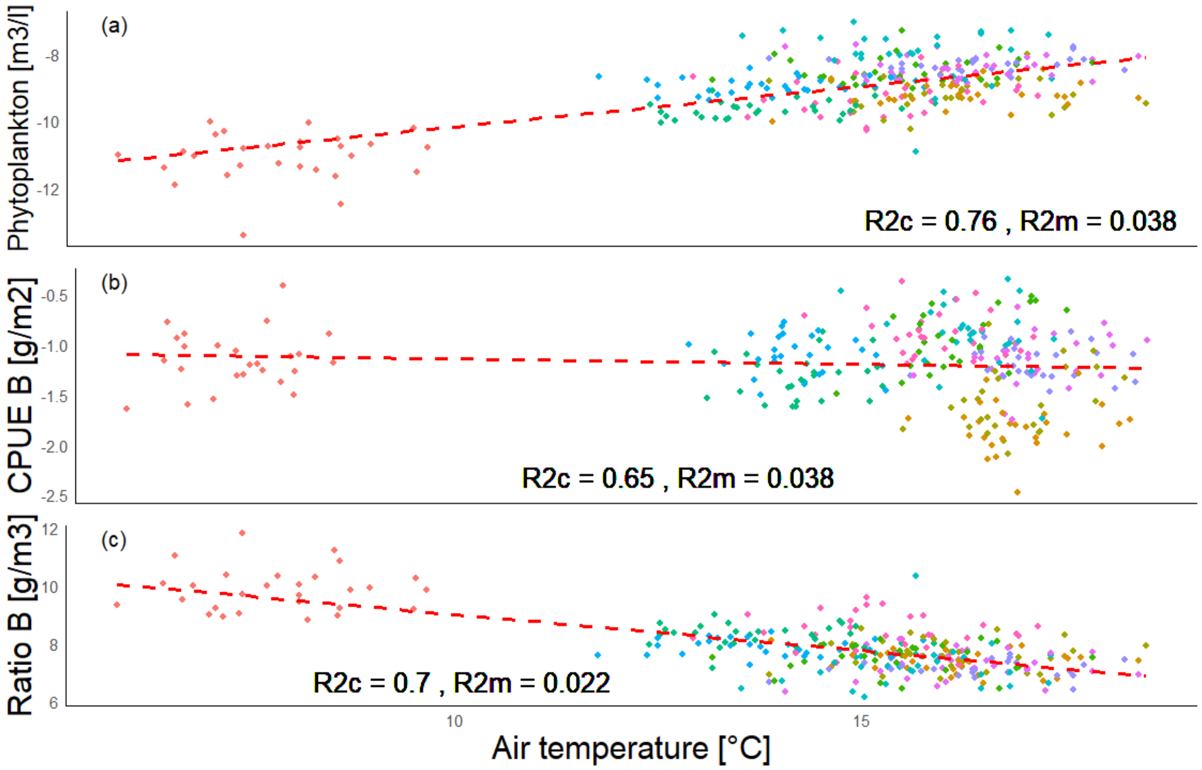

Figure 6: (a) Phytoplankton carbon mass, (b) Catch per unit effort (CPUE) in the benthic, and (c) the ratio CPUE:Phytoplankton carbon mass as a function of mean growth season air temperature (June-August). The lines are the outputs from the models including temperature, phosphorus and their interaction as explanatory variables. Phytoplankton and ratio model is with no lagged temperature, meanwhile CPUE is with lagged temperature. Lagged temperature refers to mean temperature for the previous three years. Each point corresponds to a value representing a specific year per lake. R2c stands for conditional R2-value and R2m for marginal.

Table 3: Results of the mixed-effect model analyses on the phytoplankton, catch per unit effort using benthic nets (CPUE B) and the ratio between them two, with t-values and p-value, where a p-value smaller than 0.05 is indicating significance.

	Phytoplankton t-value	**Phytoplankton p-value**	**CPUE B t-value**	**CPUE B p-value**	**Ratio B t-value**	**Ratio B p-value**
Air temperature	1.62	0.11	-0.19	0.85	-1.33	0.18
Total phosphorus	0.55	0.58	-1.070	0.29	-0.90	0.37
Interaction	-0.56	0.58	1.20	0.23	1.24	0.37

Table 4: Marginal (R^2 marg.) and conditional (R^2 cond.) coefficient of determination for the three models with biomass.

	Phytoplankton	**CPUE B**	**Ratio B**
R^2 marg.	0.038	0.038	0.022
R^2 cond.	0.76	0.65	0.70

Over the years 1994 to 2023, there are no significant changes in mean length of fish communities in the studied lakes over time (Figure 7(a); Table A3 in Appendix). Looking at the size spectrum slopes for the same time-period, four lakes show a significant decline over time (Figure 7(b) (Table A4 in Appendix)).

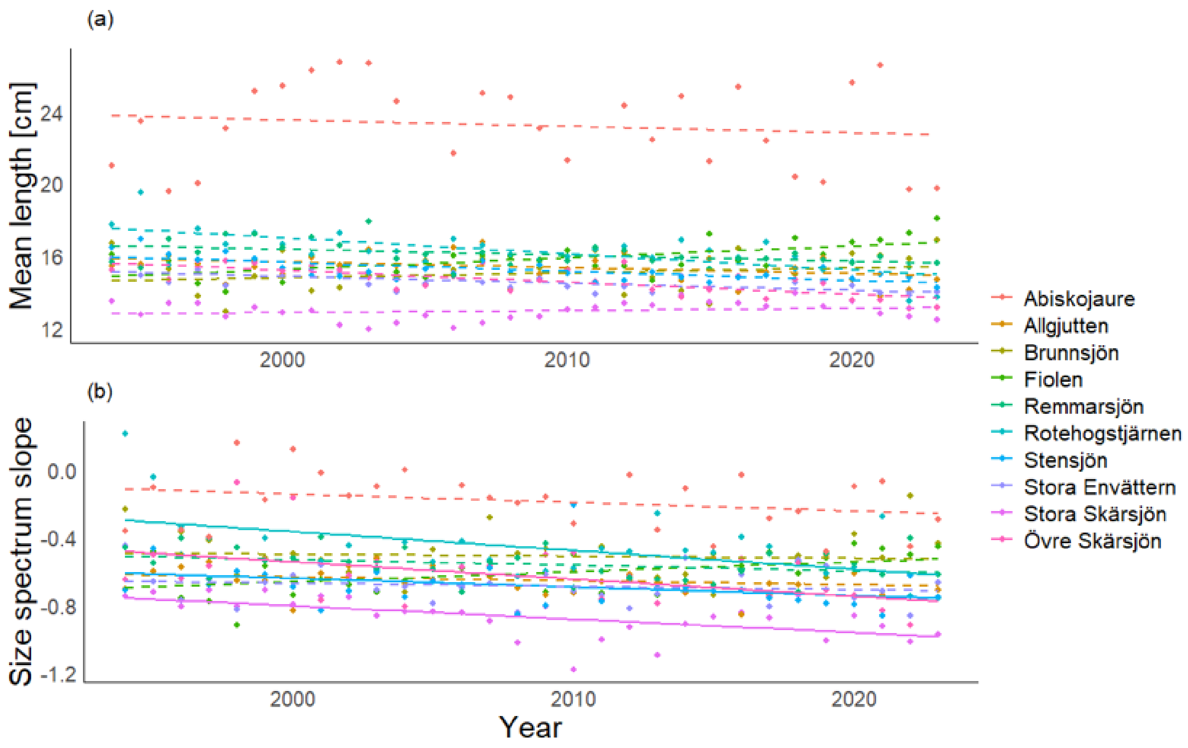

Figure 7: (a) Mean length and (b) size spectrum slope over the years 1994 to 2023 for the ten studied lakes. A solid line implies a significant relationship between the response variable and year ($p < 0.05$) and a dashed line implies a non-significant ($p > 0.05$) relationship.

Figure 8 illustrates the temporal changes in air temperature for the months June to August across the 10 lakes. Table 5 indicates that a significant change in temperature over time is observed only for Abiskojaure, with all other lakes having non-significant positive slopes.

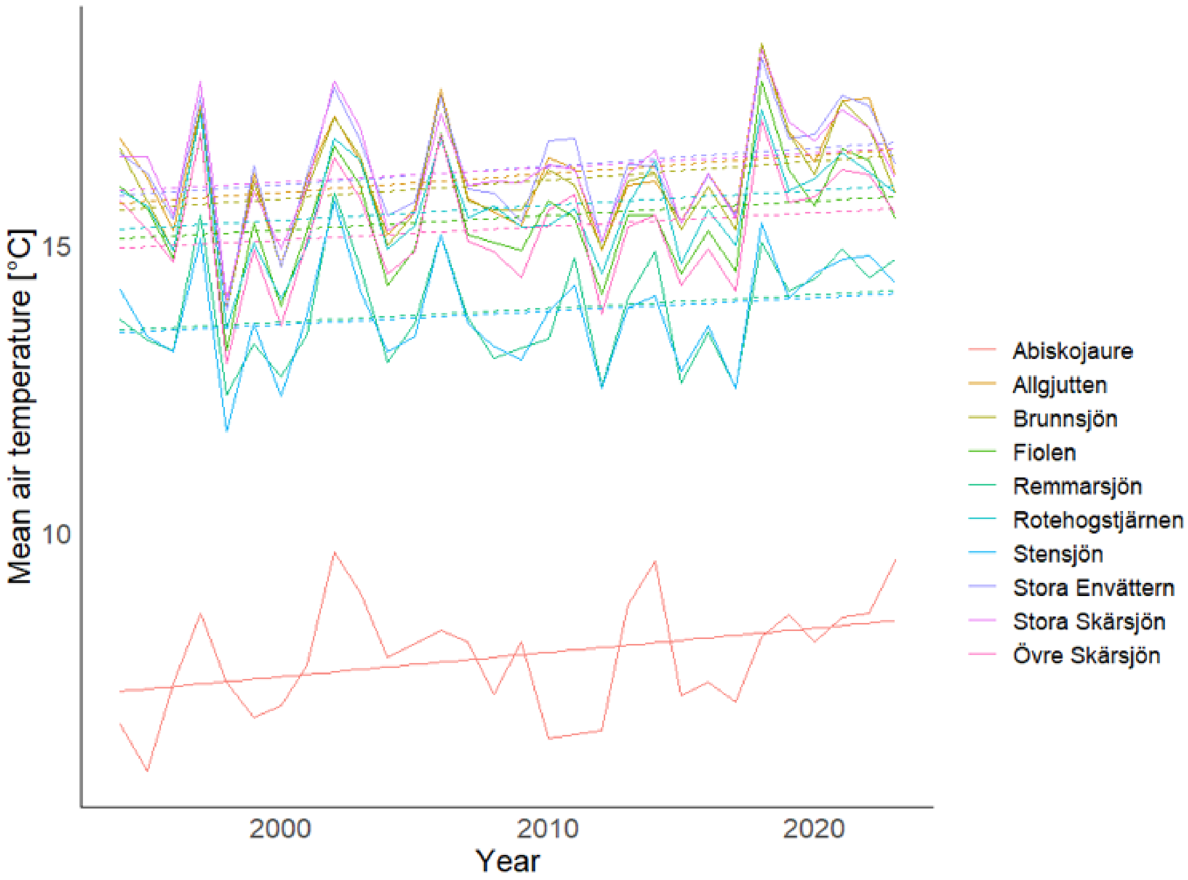

Figure 8: Mean air temperature for the months June-August for the years 1994-2023. A solid line shows a significant change for a lake over time, meanwhile a dashed line is indicating no significant trend.

Table 5: P-value and value of slope based on the regression analyses of the relationship between lakes air temperature and year.

Lake	P-value	Value of slope
Abiskojaure	0.04	0.04
Allgjutten	0.12	0.03
Brunnsjön	0.14	0.03
Fiolen	0.24	0.03
Remmarsjön	0.25	0.02
Rotehogstjärnen	0.18	0.03
Stensjön	0.25	0.02
Stora Envättern	0.13	0.03
Stora Skärsjön	0.21	0.03
Övre Skärsjön	0.27	0.02

4. DISCUSSION

This study demonstrates that temperature has a negative effect on size spectrum slopes and thus the relative biomass of large relative to small individuals, indicating a shift towards smaller individuals. Accordingly, also mean body size declined with temperature. The effect of temperature holds both in nutrient-rich and nutrient-poor lakes, indicating that temperature can affect the fish community size spectra and mean body size in a predictable way across different types of lakes. This is evident in that no significant effects on size spectrum slopes or mean body size are observed as a result of variation in total phosphorus concentration or the interaction between temperature and total phosphorus. In contrast to the size spectrum slopes, neither phytoplankton nor catch per unit effort of fish biomass or their ratio varied with temperature in this study. This gives an indication on that size spectra may be a better indicator when looking at food web responses to climate warming than only looking at biomasses. Not only because it seems to respond more to variation in temperature, but also because it provides a method to compare size distributions and indicate energy transfer efficiency, which may also be challenged by climate change (Atkinson et al. 2024).

The results partly agree with the hypothesis of this study. In line with the hypothesis, it is found that the size spectrum slope decreases with temperature. The results suggests that climate warming is likely to both decrease mean body size in lake fish communities, and lead to a relative increase in small-bodied relative to larger fish (similar to Arranz et al. 2023). Yet, the absence of a notable negative trend in mean length over time for the observed lakes contradicts the hypothesis of that gradual warming would already have caused noticeable changes. This could either imply random chance overriding the temperature effect and/or that it is difficult to detect such changes within lakes over the time-period that is studied, supported by many non-significant positive trends in temperature over time in the study lakes. Other factors than temperature that can influence mean body size and size spectra over time can be fishing pressure, invasive species and other factors affecting species composition. Still, temperature has a significant effect on the size spectrum slope when analyzed across the 10 study lakes.

The findings of this study highlight the complexity of ecosystem responses to environmental, anthropogenic, and biological changes, suggesting that other factors may play a role in affecting temporal change of size spectrum slopes and mean body size. Still, over long time-periods, as temperatures will continue to rise (Intergovernmental Panel on Climate Change (IPCC) 2023), the results suggest that fish community size spectra slopes will continue to decline. A declining size spectrum slope over time could indicate a deterioration in trophic transfer efficiency, affecting the entire food web, including production of top predators such as predatory fishes (Marin et al. 2023). This is because larger individuals may struggle more to meet their need of energy, potentially reducing growth efficiency and further decreasing the size spectrum slope (Arranz et al. 2021; Atkinson et al 2024). Other factors that can affect shifts in distribution and declines in body size are oxygen-limitation and changes in species composition. In warmer temperatures, smaller species may thrive and complete their life cycles more quickly, which can affect fish community size distributions (Jeppesen et al. 2012), and long-term contribute to further shifts in fish community size spectra. Another factor impacting size distributions is fishing (Arranz et al. 2023), which often selectively removes larger fishes (Baudron et al. 2013). Additionally, warmer environments can lead to earlier maturation at smaller size of fish (Niu et al. 2023), which can affect the size distribution within communities by lowered body growth rates after maturation. Also, changes in species composition and prey-predator dynamics could add to disrupting energy transfer within food webs, and thus increase the risk of population collapses and loss of ecosystem functions (Gårdmark & Huss 2020). This is highlighting the complexity of environmental variables affecting lake ecosystems.

Interestingly, whereas it was found that the size spectrum slope and mean body size are negatively affected by temperature, phytoplankton biomass and fish catch per unit effort

(CPUE) showed no relationship with temperature. This underscores the importance of selecting appropriate indicators when assessing climate change-induced changes. Still, we know that phytoplankton are directly influenced by temperature (Grimaud et al. 2015) and there is strong evidence that they easily adapt to climate change (Sauterey et al. 2023). A larger set of lakes may be necessary to identify a significant relationship between phytoplankton and temperature dynamics (given that there indeed is a trend towards more phytoplankton with higher temperature, although non-significant). This could mean that while phytoplankton might adapt to changing temperatures, the larger individuals of fish in the ecosystem do not adapt so easily. The well-established relationship between phosphorus and phytoplankton suggests that additional lake data may be necessary to detect significant correlations.

Additional lake data may also be necessary to further investigate the findings suggesting that climate warming is likely to decrease the mean body size in lake fish communities. However, given the space-for-time design, these conclusions are drawn from comparing lakes with different mean temperatures rather than observing temporal changes within each lake. So, whereas this is suitable to infer spatial variation, this method limits the interpretation of what has happened within individual lakes over time. For further studies, it would be beneficial to conduct within-lake correlation analyses to directly examine how temperature changes correlate with changes in fish size within each lake. Care should be exercised when interpreting changes between lakes as indicative of changes within lakes over time, due to the unique conditions, ecological dynamics, and human influences present in each lake. Comparing different lakes may not accurately reflect the temporal changes within a single lake. Therefore, including a larger set of lakes with a more even temperature distribution could provide clearer results of how temperature influences size distributions of fish communities.

The stronger relationship observed between size spectra and temperature, especially across lakes, could indicate future changes over time in several lakes. This study indicates that size spectrum slopes could be a valuable complement to use as an indicator of climate change impacts. At the same time, the analysis of temperature trends across the studied lakes provides further insights into the localized impacts of climate warming on freshwater ecosystems (Table 5). While Abiskojaure shows a significant warming trend, the absence of significant trends in other lakes suggest a more nuanced analyses of temperature dynamics and additional study years may be needed to fully evaluate the effects of temperature change on fish community size spectra.

Looking at the results, it seems that the coldest lake, Abiskojaure, exerts a disproportionate influence on the statistical analysis of size spectrum slopes and mean body size. Conducting a sensitivity analysis by excluding Abiskojaure and examining the resulting changes in trend significance could provide valuable insights into the robustness of the findings. Accordingly, when testing the models without Abiskojaure, no significant effects of the explanatory variables are found (results not shown), suggesting that Abiskojaure has a unique influence. A comparative analysis between Abiskojaure and the other lakes, exploring long-term trends using alternative statistical methods, could contribute to a more comprehensive understanding of temperature impact across the lake ecosystems. Integrating additional environmental variables would also be an alternative. However, removing Abiskojaure from the analysis would lead to loss of valuable data and insights relevant also in cold-water ecosystems.

Therefore, careful consideration is needed when interpreting the results and making decisions regarding data inclusion or exclusion. This further supports the value of studying more lakes covering the entire temperature gradient.

The limited selection of predetermined trend lakes could also have implications for the obtained results. The studied trend lakes are part of the Swedish Freshwater monitoring program, in place to evaluate larger-scale impacts and assess environmental quality on lake ecosystems (Havs- och vattenmyndigheten 2014). However, these lakes may not be entirely representative of all lake ecosystems in Sweden. Compared to many of the marine systems, lake ecosystems are generally less impacted by fishing. This makes fish in lakes good study objects to study the influence of environmental factors, such as climate and temperature, on size spectra without the results being heavily influenced by fishing. Understanding the factors shaping fish community size spectra and mean body size can help us understand resilience of freshwater ecosystems to climate warming and changes in nutrient availability.

Both temperature and total phosphorus is included in the analyses because a lake is rarely affected by just one stressor (Bouraï et al. 2020). Linear mixed-effects models are used to gain insight into how temperature affects ecosystem structure and to account for random lake effects. This study primarily focuses on natural variations in temperature, which can also be inferred to reflect long-term changes over time. To account for delayed ecological responses, temperature data were lagged by three years, which could affect the results. When analyzing ten trend lakes scattered across Sweden (but predominantly situated in the warmer southern Sweden), a linear mixed-effects model with random effects allows for consideration of each lake’s unique initial conditions, and therefore provides a more accurate estimate of fixed effect and their uncertainties. The nesting of years within lakes acknowledges the variability in time’s impact across lakes. Understanding these interactive effects is crucial for precise statistical modeling. Incorporating total phosphorus as a covariate and the interaction between temperature and total phosphorus in the linear mixed-effects models can improve model accuracy and allow for testing temperature effects while controlling for another major environmental factor known to influence lake ecosystem. As for the approach to estimate size spectra, I used bins with log2-transforming. An alternative approach to look at climate change affecting fish community size spectra could be to use the Maximum Likelihood Estimation (MLE) method (Edwards et al. 2017) instead of the binning method. In further research, it could be of importance to assess the impact on size spectra using a range of methods, especially if it is used as an ecosystem indicator. This study focused on a limited number of lakes in Sweden, but its methodologies and findings can be applicable to other temperate freshwater ecosystems globally.

It is challenging for statistical models to accurately predict how ecosystem is affected of different human pressures, and their results vary widely among them in terms of causes, extent, and regional effects (Atkinson et al. 2024). Due to the complexity of ecosystems, accurate predictions concerning climate change impacts are generally difficult. One limitation is that it is difficult to include all parameters that can affect the response variables (and not appropriate in hypothesis testing), and at the same time avoiding making it to complicated. Another potential limitation is that there are 17 species of fish represented and some species can weigh less than 8g but be bigger than the length limit for these weights, affecting the result of mean body size. An additional limitation is the challenge of obtaining a comprehensive picture of a lake´s fish community using selective catch methods. Net catches, being a passive method, have inherent limitations that must be considered when analyzing data (FINFO 2001). These limitations include the size and composition of catches, which depend, among other things, on fish activity, weather conditions, water temperature and mesh size. This is especially important when estimating parameters relating to body size, as the nets often do not catch the smallest fish, potentially leading to underestimation of the abundance of smaller size classes when calculating size spectrum slopes. Consequently, it is difficult to correctly estimate the size composition and biomass of the whole fish community and certain species in the lakes, as the nets for example can overrepresent larger fishes. An attempt was made to overcome this by setting the number of bins and binning size in order to ensure uniform representation of the size classes (similar to Marin et al. 2023).

To gain deeper understanding of how different human pressures may influence the effect of temperature, additional models could be tested with explanatory variables other than temperature and phosphorous. This not only enhances our understanding but also underscores the importance of incorporating size spectrum analysis into broader assessment of lake ecosystem health and resilience, while considering other stressors that can affect the fish distribution. Current approaches including numbers and biomasses are still valid methods, but they could be complemented with size spectra, specifically to assess impacts on lake fish communities and their functioning. Size spectrum analysis also provides a promising approach to look at the effects of complex interactions on energy and nutrient fluxes in ecosystems, influenced by climate change and other human pressures.

This study offers valuable insights for municipal and regional administrations involved in the management of nutrient levels and water quality in lake ecosystems. For example, the study highlights the complex relationship between temperature, phosphorus levels and fish communities. While nutrient management remains crucial for maintaining water quality, climate-induced changes in temperature may have a more pronounced impact on fish communities according to this study. However, this does not diminish the importance of limit human-caused nutrient inputs.

To address nutrient inputs, municipal and regional authorities can implement several strategies. One effective method is establishing buffer strips composed of natural vegetation and implemented along waterways to absorb nutrients from agricultural runoff before they reach lakes (Vought et al. 1995). These buffer strips help prevent excessive nutrient leaching into both groundwater and surface water, thereby the buffer strips can contribute to reducing the total amount of nutrients that end up in lakes. For example, as much as 95% of the phosphorus load, usually attached to sediment, can be reduced by a buffer strip that is 10 m wide (Vought et al. 1995). Another solution to nutrient inputs involves constructing large wetlands, which can help mitigate nutrient levels in runoff water in catchment areas before it reaches lake ecosystems, thereby improving water quality (Borgström et al. 2024). An additional solution to decrease nutrient input in lake ecosystems is to treat wastewater using a method called biological nutrient removal before it is released into the environment (Wainaina et al. 2021). This method typically uses microbes for uptake of phosphorus and nitrogen. Phosphorus is absorbed because the microbes specifically used for phosphorus rely on phosphate for their metabolic functions, operating under altering anaerobic and aerobic conditions (Shen Lee et al. 2014). According to Wainaina et al. (2021), phosphorus levels can decrease from 15 mg/L in the inflow to as low as 0.1 mg/L in the outflow from wastewater treatment using the biological nutrient removal method. Implementing these strategies can help manage nutrients inputs, thereby contributing to healthier lake ecosystems and providing a foundation for policy decisions.

The findings of this study can guide policy decisions related to lake management by municipal and regional authorities. These decisions may involve setting limits on nutrients and implementing habitat restoration projects. Furthermore, by incorporating size spectrum analysis into broader assessments of lake ecosystem health, municipal and regional administrations can enhance their ability to effectively manage and conserve freshwater resources. This can equip them to address ongoing environmental challenges more comprehensively and make decision about e.g. conservations strategies, as well as land-use planning. There is a growing recognition of the need to consider both societal and scientific needs, as in today's national monitoring programs of lakes in Sweden (Fölster et al. 2014). These programs provide invaluable data of water chemistry and biological measures, for some parameters spanning 50 years. Such data are essential for establishing reference conditions and tracking the health and recovery of lake ecosystems. Declines in size spectrum slopes and mean body size can lead to significant changes in structure and function of fish communities, potentially affecting the vital ecosystems services they provide. For example, a decrease in the average size of fish can reduce the total biomass available for human consumption. Therefore, monitoring and managing size distributions in a standardized way are essential to sustain these valuable ecosystem services in the face of environmental change.

Future studies should focus on gaining a better understanding of the underlying mechanisms driving changes in size spectra and mean body size, such as the effects of temperature on growth rates, and how these changes impact ecosystems, their capacity to maintain biodiversity, ensure overall stability, and enhance resilience to further climate change. Another important area for study would be to investigate changes in biomass across trophic levels for a larger set of lakes, such as phytoplankton and fish biomass (as in this study). Also, what that say about trophic transfer efficiency, and how that is affected by human pressures. Additionally, there is a need to develop new and innovative approaches to support sustainable management of aquatic ecosystems. These approaches should enhance climate adaptation strategies for the aquatic ecosystems so humans can continue using the natural resources they provide in a way that do not compromise the ability of future generations to meet their own needs.

5. CONCLUSION

The main findings of this study are that temperature negatively affects size spectrum slopes and mean body size, with these effects observable across both nutrient-rich and nutrient-poor lakes. In contrast, the analyses of the 10 Swedish trend lakes revealed no significant impact on phytoplankton biomass, catch per unit effort of fish biomass, or their ratio. Trend analyses also show that the size spectrum slope is decreasing over time in some but not in all the studied lakes. The results suggest that size spectra may be a reliable indicator for assessing climate change effects on freshwater ecosystems, and specifically on fish communities. Understanding these relationships is crucial due to the essential ecosystem functions and services that fish provide, such as food provision, nutrient cycling, climate regulation and recreational activities. The study contributes to the growing body of evidence that climate warming is reshaping fish communities and aquatic ecosystems. With the human population growing and with rapid changes occurring in aquatic ecosystems due to climate change, there is increasing pressure from factors such as exploitation and land use, potentially interacting with the pressure of climate change. Continued monitoring of fish body size, and new analyses of size spectra, can help us understand how climate change could affect ecosystem dynamics over time and especially provide insight into future changes in fish communities. As human pressures on aquatic ecosystems increase, it becomes crucial to ensure that solutions, management strategies and conservation efforts are in place to anticipate and manage ecological complexities, ensuring their sustainable use and resilience.

6. REFERENCES

Aguilar-Alberola, J. & Mesquita-Joanes, F. (2014). *Breaking the temperature-size rule: Thermal effects on growth, development and fecundity of a crustacean from temporary waters.* Journal of Thermal Biology. 42, 15-24. https://doi.org/10.1016/j.jtherbio.2014.02.016

Ahlkrona, M. (2002). *Phosphorus in a Biogeochemical Lake Model.* Swedish Meteorological and Hydrological Institute. RH No. 17. ISSN 0283-1104.

Andersen, K. H., Jacobsen, N. S. & Farnsworth. K. D. (2016). *The theoretical foundations for size spectrum models of fish communities.* Canadian Journal of Fisheries and Aquatic Sciences. 73(4), 575-588. https://doi.org/10.1139/cjfas-2015-0230

Appelberg, M. (2000). *Swedish Standard Methods for Sampling Freshwater Fish with Multi-Mesh Gillnets.* Fiskeriverket Information 2000:1. ISSN 1402-9719.

Arranz, I., Brucet, S., Bartrons, M., García-Comas, C. & Benejam, L. (2021). *Fish size spectra are affected by nutrient concentration and relative abundance of non-native species across streams of the NE Iberian Peninsula.* Science of The Total Environment. 795, 15. https://doi.org/10.1016/j.scitotenv.2021.148792

Arranz, I., Grenouillet, G. & Cucherousset, J. (2023). *Human pressures modulate climate-warming-induced changes in size spectra of stream fish communities.* Nat Ecol Evol. 7, 1072-1078. https://doi.org/10.1038/s41559-023-02083-z

Atkinson, A., Rossberg, A.G., Gaedke, U. et al. (2024). *Steeper size spectra with decreasing phytoplankton biomass indicate strong trophic amplification and future fish declines.* Nat Commun. 15, 381. https://doi.org/10.1038/s41467-023-44406-5

Baudron, A., Needle, C., Rijnsdrop, A.D. & Marshall, C.T. (2013). *Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes*. Global Change Biology. 20(4), 1023-1031. https://doi.org/10.1111/gcb.12514

Benoît, E. & Rochet, M-J. (2003). *The meaning of fish size spectra, the effects of fishing on them and the usefulness of their slope as indicator of fishing impacts.* International Council for the Exploration of the Sea. ICES CM 2003/N:05.

Benstead, J. P., Hood, J. M., Whelan, N. V., Kendrick, M. R., Nelson, D., Hanninen, A. F. & Demi, L. M. (2014). *Coupling of dietary phosphorusand growth across diverse fish taxa: a meta-analysis of experimental aquaculture studies.* Ecology. 95(10), 2768-2777. https://doi.org/10.1890/13-1859.1

Blomqvist, P., Bell, R. T., Olofsson, H., Stensdotter, U. & Vrede, K. (1994). *Plankton and water chemistry in Lake Njupfatet before and after liming.* Can. J. Fish. Aquat. Sci. 52, 551-565. Printed in Canada.

Boltaña, S., Sanhueza, N., Aguilar, A., Gallardo-Escarate, C., Arriagada, G., Valdes, J. A., Soto, D. & Quiñones, R. A. (2017). *Influences of thermal environment on fish growth.* Ecology and Evolution. 7(17), 6814-6825. https://doi.org/10.1002/ece3.3239

Borgström, A., Hansson, L-A., Klante, C. & Sjöstedt, J. (2024). *Wetlands as a potential multifunctioning tool to mitigate eutrophication and brownification.* Ecological Applications. 34(2), e2945. https://doi.org/10.1002/eap.2945

Bouraï, L., Logez, M., Laplace-Treyture, C. & Argillier, C. (2020). *How Do Eutrophication and Temperature Interact to Shape the Community Structures of Phytoplankton and Fish in Lakes?* Water. 12(3), 779. https://doi.org/10.3390/w12030779

Britannica, T. Editors of Encyclopedia. *trophic level.* Encyclopedia Britannica. https://www.britannica.com/science/trophic-level [2024-05-22]

Canosa L.F. & Bertucci, J.I. (2023). *The effect of environmental stressors on growth in fish and its endocrine control.* Front Endocrinol (Lausanne). 14. https://doi.org/10.3389/fendo.2023.1109461

Cochrane, K. L. (2002). *A Fishery Manager's Guidebook - Management Measures and Their Application*. [book]. FAO – Food and Agriculture Organization of the United Nations. ISBN: 9251047731

Czamanski, M., Nugraha, A., Pondaven, P., Lasbleiz, M., Masson, A., Caroff, N., Bellail, R. & Tréguer, P. (2011). *Carbon, nitrogen and phosphorus elemental stoichiometry in aquacultured and wild-caught fish and consequences for pelagic nutrient dynamics.* Mar Biol. 158, 2847-2862. https://doi.org/10.1007/s00227-011-1783-7

Dolbeth, M., Cusson, M., Sousa, R. & Pardal, M.A. (2012). *Secondary production as a tool for better understanding of aquatic ecosystems.* Canadian Journal of Fisheries and Aquatic Sciences. 69(7), 1230-1253. https://doi.org/10.1139/f2012-050

van Dorst, R.M., Argillier, C., Brucet, S., Holmgren, K., Volta, P., Winfield, I.J. & Mehner, T. (2022). *Can size distributions of European lake fish communities be predicted by trophic positions of their fish species?* Ecology and Evolution. 12(7), e9087. https://doi.org/10.1002/ece3.9087

Drakare, S. (2021). *Undersökningstyp: Växtplankton i sjöar.* (Verision 1.5: 2021-06-24) Havs- och vattenmyndigheten.

Edwards, A.M., Robinson, J.P.W., Plank, M.J., Baum, J.K. and Blanchard, J.L. (2017), *Testing and recommending methods for fitting size spectra to data*. Methods Ecol Evol, 8(1), 57–67. https://doi.org/10.1111/2041-210X.12641

Elser, J. J., Andersen, T., Baron, J. S., Bergström, A., Jansson, M., Kyle, M., Nydick, K. R., Steger, L. & Hessen, D. O. (2009). *Shifts in Lake N:P Stoichiometry and Nutrient Limitation Driven by Atmospheric Nitrogen Deposition.* Science. 326(5954), 835-837. https://www.science.org/doi/10.1126/science.1176199

FINFO - Fiskeriverket informerar (2001). *Standardiserad metodik för provfiske i sjöar.* Drottningholm: Fiskeriverket. 2001:2.

Froese, R. & Pauly, D. (2022). FishBase. www.fishbase.se

Fölster, J., Johnson, R.K., Futter, M.N. & Wilander, A. (2014). *The Swedish monitoring of surface waters: 50 years of adaptive monitoring.* AMBIO. 43(Suppl 1), 3–18. https://doi.org/10.1007/s13280-014-0558-z

Fölster, J. & Stensdotter Blomberg, U. (2016). *Vattenkemi i sjöar.* (Verision 1:2, 2016-11-01). Havs- och vattenmyndigheten.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. (2001). *Effects of size and temperature on metabolic rate*. Science, 293, 2248–2251. https://www.science.org/doi/10.1126/science.1061967

Grimaud, G. M., Le Guennec, V., Ayata, S-D., Mairet, F., Sciandra, A. & Bernard, O. (2015). *Modelling the effects of temperature on phytoplankton growth across the global ocean.* IFAC-PapersOnLine. 48(1), 228-233. https://doi.org/10.1016/j.ifacol.2015.05.059

Gårdmark, A. & Huss, M. (2020). *Individual variation and interactions explain food web responses to global warming.* Philosophical Transactions of The Royal Society B: Biological Sciences. 375(1814). https://doi.org/10.1098/rstb.2019.0449

Hammerschlag, N., Schmitz, O. J., Flecker, A. S., Lafferty, K. D., Sih, A., Atwood, T. B., Gallagher, A. J., Irschick, D. J., Skubel, R. & Cooke, S. J. (2019). *Ecosystem Function and Services of Aquatic Predators in the Anthropocene.* Trends in Ecology & Evolution. 34(4), 369–383. https://doi.org/10.1016/j.tree.2019.01.005

Havs- och vattenmyndigheten. (2014). *Miljöövervakningens programområde Sötvatten.* https://www.havochvatten.se/overvakning-och-uppfoljning/miljoovervakning/organisation-och-programomraden/miljoovervakningens-programomrade-sotvatten.html [2024-05-13].

HELCOM – Helsinki Commission (n.d.). *Fish Communities.* Baltic Marine Enviroment Protection Commission. https://helcom.fi/action-areas/fisheries/fish-communities/ [2024-05-22]

Helsel, D. R., Hirsch, R. M., Ryberg, K. R., Archfield, S. A. & Gilroy, E. J. (2020). *Statistical Methods in Water Resources.* Reston, VA: U.S. Geological Survey.

Holmlund, C.M. & Hammer, M. (1999). *Ecosystem services generated by fish populations.* Ecological Economics. 29(2), 253-268. https://doi.org/10.1016/S0921-8009(99)00015-4

Hui, D. (2012). *Food web: Concept and Applications.* Nature Education Knowledge. 3(12), 6.

Huser, B. J., Futter, M. N., Wang, R. & Fölster, J. (2018). *Persistent and widespread long-term phosphorusdeclines in Boreal lakes in Sweden.* Science of The Total Environment. 613-614, 240-249. https://doi.org/10.1016/j.scitotenv.2017.09.067

Intergovernmental Panel on Climate Change (IPCC). (2023). *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. [Core Writing Team, H. Lee, and J. Romero (eds.)]. IPCC, Geneva, Switzerland. 35-115. https://doi.org/10.59327/IPCC/AR6-9789291691647

Jeppesen, E., Mehner, T., Winfield, I.J. et al. (2012) Impacts *of climate warming on the long-term dynamics of key fish species in 24 European lakes.* Hydrobiologia. 694, 1-39. https://doi.org/10.1007/s10750-012-1182-1

Kuriakose, S. (2017). *Estimation of length weight relationship in fishes.* In: Course Manual Summer School on Advanced Methods for Fish Stock Assessment and Fisheries Management. Lecture Note Series No. 2/2017. CMFRI; Kochi, pp. 215-220.

Malmaeus, J. M., Blenckner, T., Markensten, H. & Persson, I. (2006). *Lake phosphorusdynamics and climate warming: A mechanistic model approach*. Ecological Modelling. 190(1-2), 1-14. https://doi.org/10.1016/j.ecolmodel.2005.03.017

Marin, V., Arranz, I., Grenouillet, G. & Cucherousset, J. (2023). *Fish size spectrum as a complementary biomonitoring approach of freshwater ecosystems.* Ecological Indicators. 146, 109833. https://doi.org/10.1016/j.ecolind.2022.109833

Mehner, T., Attermeyer, K., Brauns, M., Brothers, S., Hilt, S., Scharnweber, K., van Dorst, R. M., Vanni, M. J. & Gaedke, U. (2022). *Trophic Transfer Efficiency in Lakes.* Ecosystems. 25, 1628–1652. https://doi.org/10.1007/s10021-022-00776-3

Miljödata-MVM (2024). Swedish University of Agricultural Sciences (SLU). National data host lakes and watercourses, and national data host agricultural land, https://miljodata.slu.se/mvm/ [2024-02-01].

Nagelkerken, I., Goldenberg, S. U., Ferreira, C. M., Ullah, H. & Connell, S. D. (2020). *Trophic pyramids reorganize when food web architecture fails to adjust to ocean change.* Science. 369(6505), 829-832. https://doi.org/10.1126/science.aax0621

Nathanailides, C., Kolygas, M., Tsoumani, M., Gouva, E., Mavraganis, T. & Karayanni, H. (2023). *Addressing Phosphorus Waste in Open Flow Freshwater Fish Farms: Challenges and Solutions.* Fishes. 8(9), 442. https://doi.org/10.3390/fishes8090442

Nationalencyklopedin (NE). (n.d.). antropogen. https://www-ne-se.ezproxy.its.uu.se/uppslagsverk/encyklopedi/l%C3%A5ng/antropogen [2024-05-22]

National Register over Survey test-fishing – NORS (2024). Swedish University of Agricultural Sciences (SLU), Institution for aquatic recources. http://www.slu.se/sjoprovfiskedatabasen [2024-02-01].

National Oceanic and Atmospheric Administration (NOAA). (2024). *Climate Change: Global Temperature.* https://www.climate.gov/news-features/understanding-climate/climate-change-global-temperature [2024-05-20]

Niu, J., Huss, M., Vasemägi, A. & Gårdmark, A. (2023). *Decades of warming alters maturation and reproductive investment in fish*. Ecosphere. 14(1), e4381. https://doi.org/10.1002/ecs2.4381

Norkko, A., Villnäs, A., Norkko, J. et al. (2013). *Size matters: implications of the loss of large individuals for ecosystem function.* Scientific Reports. 3, 2646. https://doi.org/10.1038/srep02646

Petchey, O. L. & Belgrano, A. (2010). *Body-size distributions and size-spectra: universal indicators of ecological status?* Biol. Lett. 6, 434-437. https://doi.org/10.1098/rsbl.2010.0240

Reiss, J., Bridle J. R., Montoya, J. M. & Woodward, G. (2009). *Emerging horizons in biodiversity and ecosystem functioning research.* Trends in Ecology & Evolution. 24(9), 505-514. https://doi.org/10.1016/j.tree.2009.03.018

Rodgers E. M. (2021). *Adding climate change to the mix: responses of aquatic ectotherms to the combined effects of eutrophication and warming.* Biology Letters. 17(10). https://doi.org/10.1098/rsbl.2021.0442

RStudio Team. (2024). RStudio: Integrated Development Environment for R (Version 2023.12.1 Build 402) [Software]. RStudio, PBC, Boston, MA. www.rstudio.com

Sauterey, B., Le Gland, G., Cermeño, P., Aumont, O., Lévy, M. & Vallina, S. M. (2023). *Phytoplankton adaptive resilience to climate change collapses in case of extreme events – A modeling study.* Ecological Modelling. 483, 110437. https://doi.org/10.1016/j.ecolmodel.2023.110437

Shen Lee, W., Chua, A. S. M, Yeoh, H. K. & Ngoh, G. C. (2014). *A review of the production and applications of waste-derived volatile fatty acids.* Chemical Engineering Journal. 235, 83-99. https://doi.org/10.1016/j.cej.2013.09.002

Shin, Y-J., Rochet, M-J., Jennings, S., Field, J. G. & Gislason, H. (2005). *Using size-based indicators to evaluate the ecosystem effects of fishing.* ICES Journal of Marine Science. 62(3), 384-396. https://doi.org/10.1016/j.icesjms.2005.01.004

Swedish University of Agricultural Sciences (SLU). (2023). *Trend lakes.* https://www.slu.se/en/departments/aquatic-sciences-assessment/environment/environmental-monitoring-of-lakes-and-watercourses/trend-lakes/ [2024-03-19].

SMHI (2024). Gridded Precipitation and Temperature Data [PTHBV]. https://www.smhi.se/data/ladda-ner-data/griddade-nederbord-och-temperaturdata-pthbv [2024-02-29].

Swedish institute for standards (2015). SS-EN 14757:2015. Water quality - Sampling of fish with multi-mesh gillnets. Stockholm: SIS.

Vought, L. B.-M., Pinay, G., Fuglsang, A. & Ruffinoni, C. (1995). *Structure and function of buffer strips from a water quality perspective in agricultural landscapes.* Landscape and Urban Planning. 31(1-3), 323-331. https://doi.org/10.1016/0169-2046(94)01057-F

Wainaina, S., Lukitawesa & Taherzadeh, M. (2021). *Chapter Seven – Microbial Conversion of Food Waste: Volatile Fatty Acids Platform.* Current Developments in Biotechnology and Bioengineering. 205-233. https://doi.org/10.1016/B978-0-12-819148-4.00007-5

Witek-Krowiak, A., Gorazda, K., Szopa, D., Trzaska, K., Moustakas, K. & Chojnacka, K. (2022) *Phosphorus recovery from wastewater and bio-based waste: an overview.* Bioengineered. 13(5), 13474-13506. https://doi.org/10.1080/21655979.2022.2077894

Yindong, T., Xiwen, X., Miao, Q., Jingjing, S., Yiyan, Z., Wei, Z., Mengzhu, W., Xuejun, W. & Yang, Z. (2021). *Lake warming intensifies the seasonal pattern of internal nutrient cycling in the eutrophic lake and potential impacts on algal blooms*. Water Research. 188, 116570. https://doi.org/10.1016/j.watres.2020.116570

APPENDIX 1

Table A1. Coordinates, chemistry, and morphological parameters for the studied lakes. For water temperature, mean total phosphorus (TP), mean total nitrogen (TN) concentrations, absorbance at 420 nm (Abs) and air temperature, mean values are provided for the years 1994-2023, for the months June-August.

Lake	Station coordinate N/X	Station coordinate E/Y	Area [km^2]	Mean depth [m]	Max depth [m]	Water temperature [°C]	Mean TP [µg/l P]	Mean TN [µg/l N]	Abs (/5 cm)	Air temp [°C]
Abiskojaure	7581424	650600	2.838	11*	35*	10.1	4.48	788	0.419	7.86
Allgjutten	6423441	564895	0.186	11.4	40.7	19.5	7.64	415	0.0630	16.2
Brunnsjön	6272787	544705	0.107	5.3	10.6	20.0	14.3	521	0.0618	16.1
Fiolen	6327724	471494	1.646	3.8	10.5	18.9	14.4	358	0.0582	15.5
Remmarsjön	7085765	660807	1.367	5.2	14.4	17.1	10.7	508	0.292	13.9
Rotehogstjärnen	6524402	304388	0.168	3.4	9.4	19.3	19.7	465	0.0957	15.6
Stensjön	6835394	583469	0.569	4.2	8.5	18.2	7.58	385	0.178	13.8
Stora Envättern	6555227	634745	0.376	5.0	11.2	20.1	10.5	270	0.121	16.3
Stora Skärsjön	6282493	381448	0.314	3.8	11.5	19.8	11.7	306	0.184	16.3
Övre Skärsjön	6633396	530845	1.743	5.7	32	18.4	7.44	148	0.0161	15.3

* Estimated values

Table A2. Fish species found with their species-specific a and b value from FishBase for the length-weight equation $W = a * L^b$.

Species	Common name	a-value	b-value
Abramis brama	Common bream	0.00832	3.14
Alburnus alburnus	Common bleak	0.00617	3.11
Anguilla anguilla	European eel	0.000955	3.17
Coregonus albula	Vendace	0.00468	3.21
Coregonus lavaretus	Whitefish	0.00447	3.20
Ctenopharyngodon idella	Grass carp	0.00933	3.08
Cyprinus carpio	Common carp	0.0182	2.95
Esox lucius	European pike	0.00447	3.08
Gymnocephalus cernua	Eurasian ruffe	0.00977	2.99
Lota lota	Burbot	0.00525	3.04
Osmerus eperlanus	European smelt	0.00417	3.18
Perca fluviatilis	European perch	0.00977	3.09
Rutilus rutilus	Common roach	0.00794	3.15
Salvelinus alpinus	Artic char	0.00724	3.03
Sander lucioperca	Zander	0.00661	3.10
Scardinius erythrophthalmus	Common rudd	0.00832	3.15
Tinca tinca	Tench	0.0112	3.02

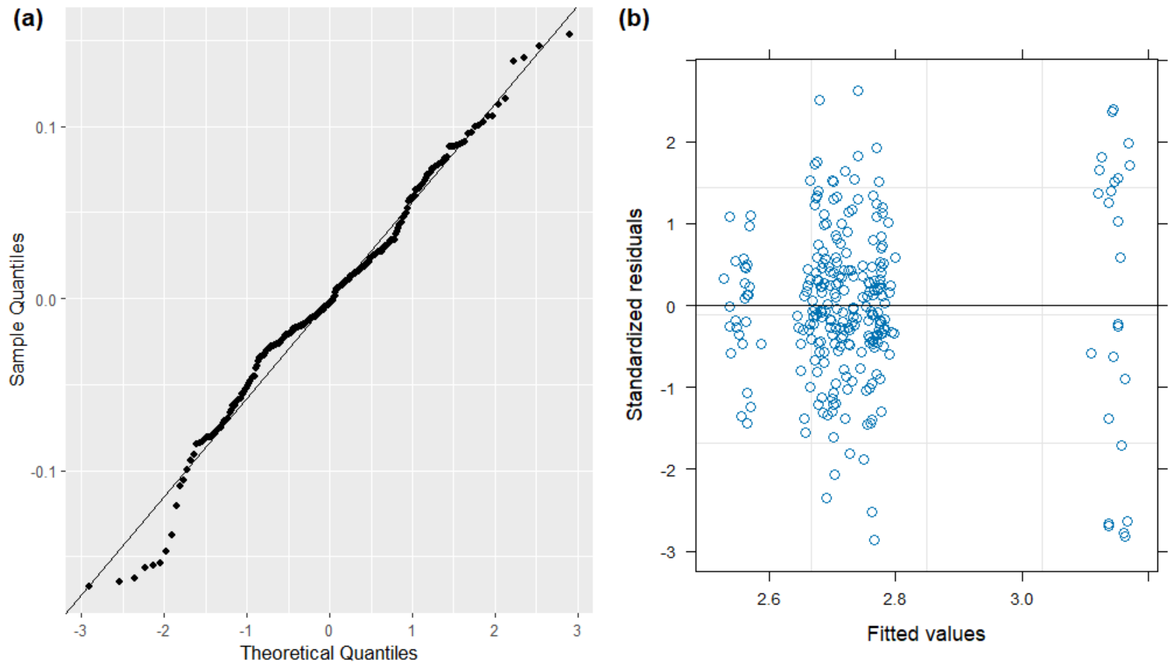

Figure A1: (a) Residual plot for the statistical model explaining mean fish length and (b) Homogeneity of variance for the same model.

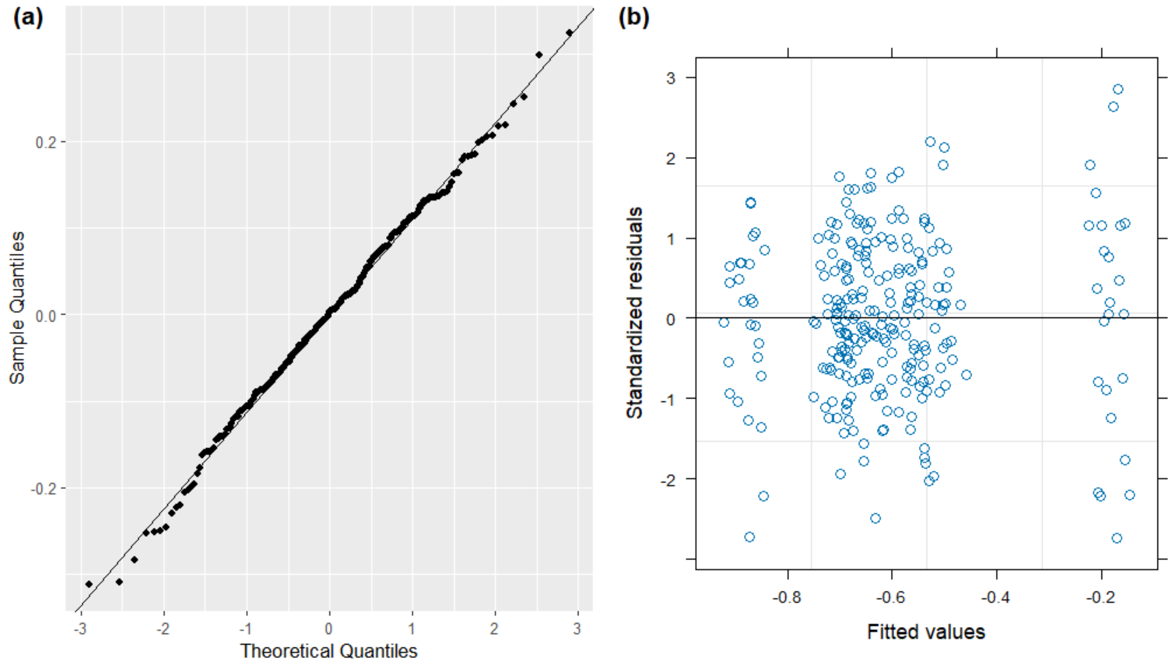

Figure A2: (a) Residual plot for the statistical model explaining size spectrum slopes and (b) Homogeneity of variance for the same model.

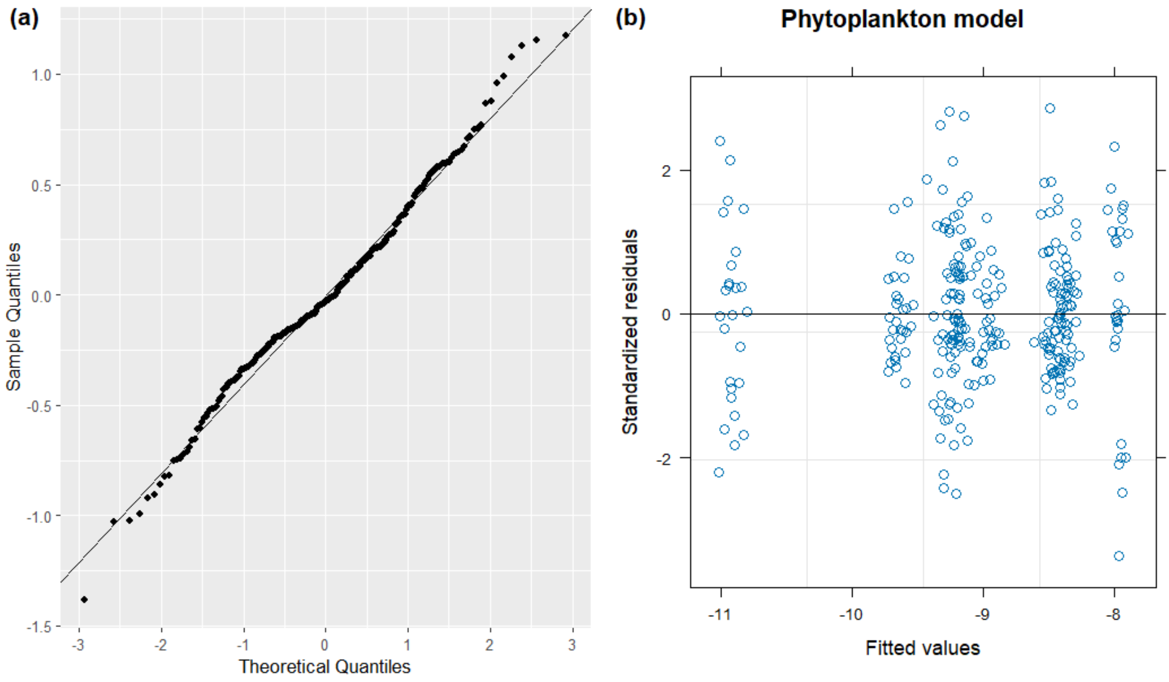

Figure A3: (a) Residual plot for the statistical model explaining phytoplankton carbon mass slopes and (b) Homogeneity of variance for the same model.

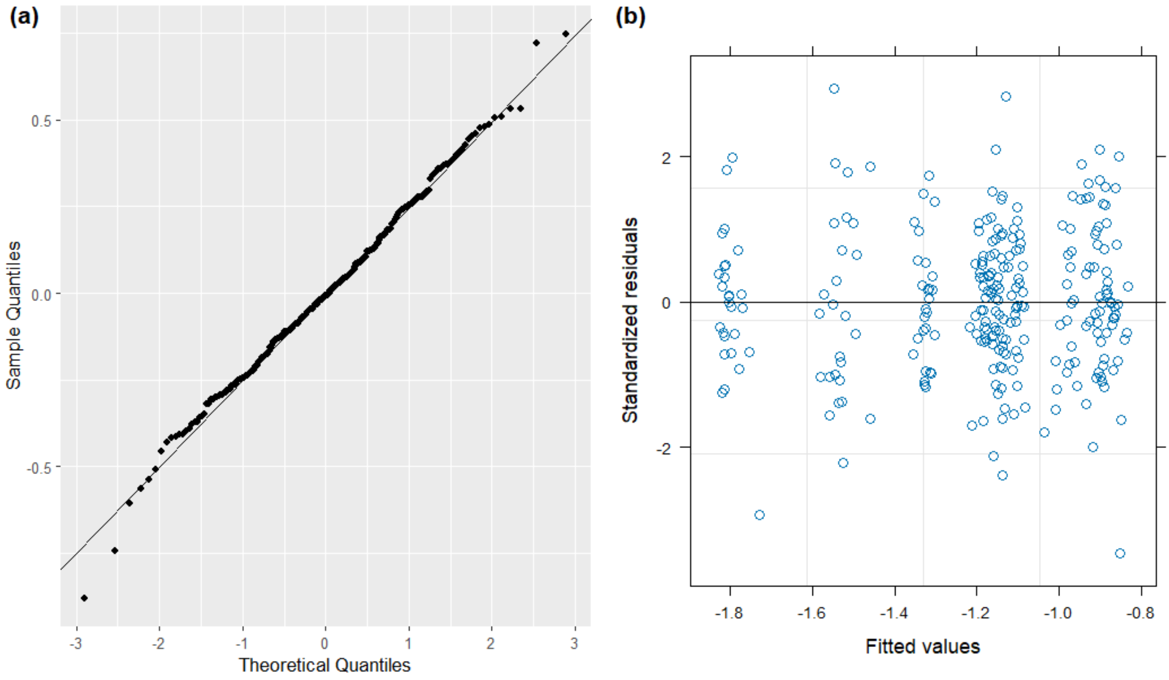

Figure A4: (a) Residual plot for the statistical model explaining catch per unit effort in the benthic of fish (CPUE B) slopes and (b) Homogeneity of variance for the same model. CPUE measures the biomass of fish caught per standard unit of fishing effort, in this case per net areas and night.

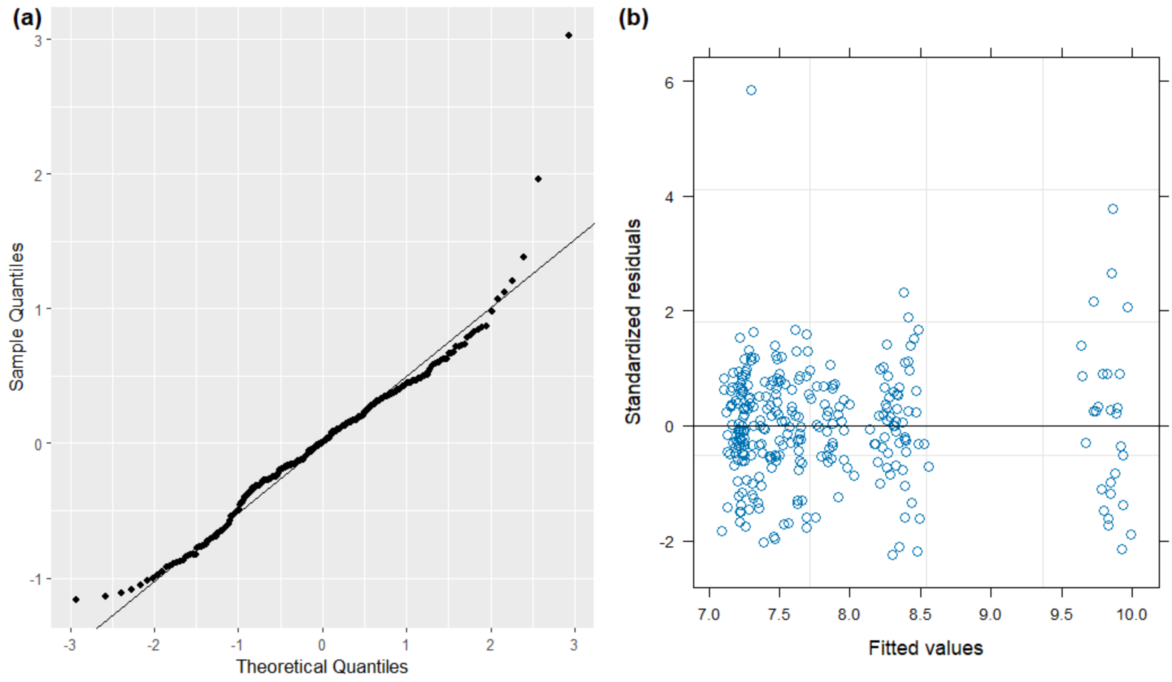

Figure A5: (a) Residual plot for the statistical model explaining the ratio, catch per unit effort in the benthic of fish (CPUE B) and phytoplankton, slopes and (b) Homogeneity of variance for the same model. Both CPUE B and phytoplankton are in carbon mass. CPUE measures the biomass of fish caught per standard unit of fishing effort, in this case per net areas and night.

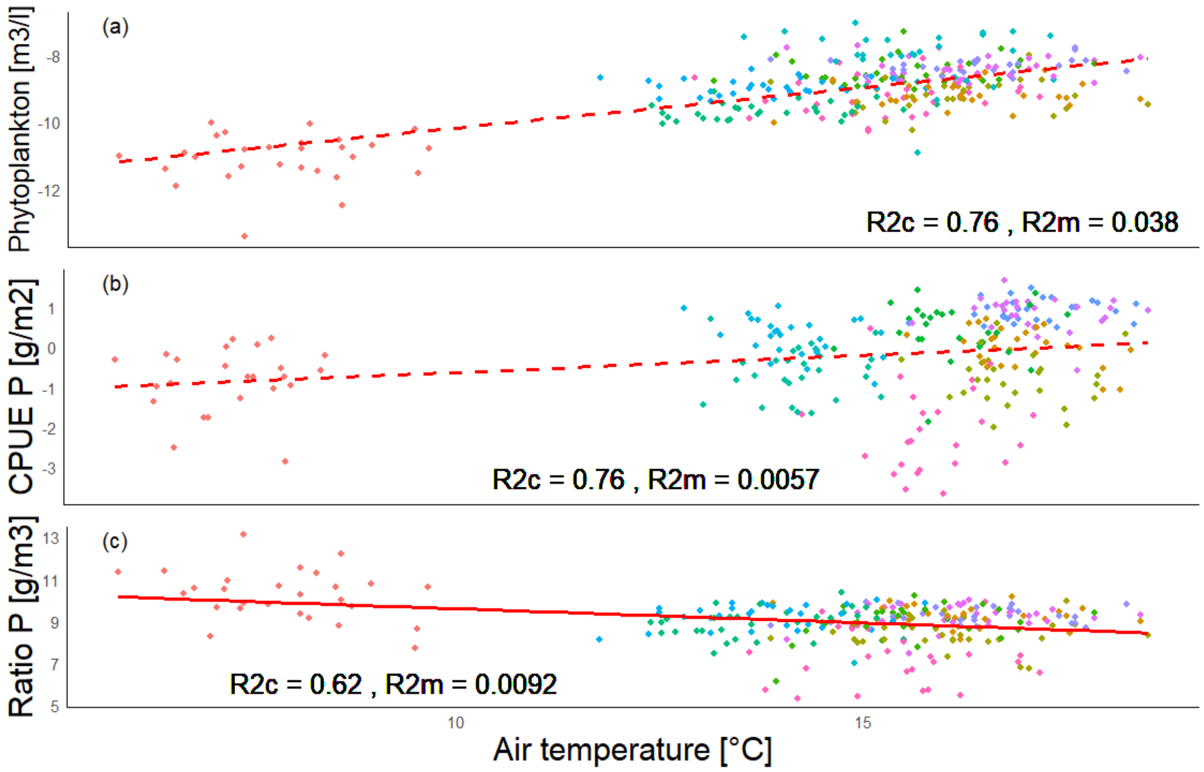

Figure A6: (a) Phytoplankton carbon mass, (b) Catch per unit effort (CPUE) in the pelagic, and (c) the ratio CPUE:Phytoplankton carbon mass as a function of mean growth season air temperature (June-August). The lines are the outputs from the models including temperature, phosphorusand their interaction as explanatory variables. Phytoplankton and ratio model is with no lagged temperature, meanwhile CPUE is with lagged *temperature. Lagged temperature refers to mean temperature for the previous three years. Each point corresponds to a value representing a specific year per lake. R2c stands for conditional R2-value and R2m for marginal.*

Table A3: P-values and regression slope from the relationship between mean length and year.

Lake	p-value	Value of slope
Abiskojaure	0.11	-0.037
Allgjutten	0.76	-0.034
Brunnsjön	0.89	0.030
Fiolen	0.48	0.065
Remmarsjön	0.46	-0.033
Rotehogstjärnen	0.62	-0.089
Stensjön	0.86	-0.050
Stora Envättern	0.47	-0.039
Stora Skärsjön	0.52	0.012
Övre Skärsjön	0.45	-0.065

Table A4: P-values and regression slope from the relationship between size spectrum slope and year.

Lake	p-value	Value of slope
Abiskojaure	0.24	-0.005
Allgjutten	0.74	-0.0023
Brunnsjön	0.43	-0.0012
Fiolen	0.36	0.006
Remmarsjön	0.95	-0.0033
Rotehogstjärnen	0.0013	-0.011
Stensjön	0.00029	-0.0051
Stora Envättern	0.47	-0.0019
Stora Skärsjön	0.017	-0.0079
Övre Skärsjön	0.020	-0.10

APPENDIX 2

The following script shows the code used to create the main statistical linear mixed effect models. The same procedure was made for each of the five models with response variables: size spectrum slope, mean body size, phytoplankton, CPUE and the ratio between CPUE and phytoplankton. The code shows for the example with size spectrum slope model. Also, the script shows the code used to create Figure 5, which is showing mean length and size spectrum slope over the years 1997 to 2023 for the ten studied lakes.

```
Size spectra with lagged ——————————-

THE_size_spectra_model_lagged <- lme(size_spectra_slope_value ~
lagged_airtemp_june_aug + lagged_tp_jun_aug +
lagged_airtemp_june_aug:lagged_tp_jun_aug, data = lagged_data, random = ~ 1
+ year | lake)

#Remove outliers for THE size spectra model
outliers_size_lagged <- abs(resid(THE_size_spectra_model_lagged)) > 3 *
sd(resid(THE_size_spectra_model_lagged))

#Make a new dataframe but without outliers
outliers_size_data_lagged <- lagged_data[!outliers_size_lagged, ]


# New model without outliers
no_outliers_THE_size_spectra_model_lagged <- lme(size_spectra_slope_value ~
lagged_airtemp_june_aug + lagged_tp_jun_aug +
lagged_airtemp_june_aug:lagged_tp_jun_aug, data =
outliers_size_data_lagged, random = ~ 1 + year | lake)

summary(no_outliers_THE_size_spectra_model_lagged)


#Normality Test
shapiro.test(resid(no_outliers_THE_size_spectra_model_lagged))

#Normally distributed?
qqnorm(resid(no_outliers_THE_size_spectra_model_lagged), main = “Size
spectrum ~ Air temp + TP + Air temp:TP”)
qqline(resid(no_outliers_THE_size_spectra_model_lagged))

#Homogeneity of variances
size_sprectra_plot <- plot(no_outliers_THE_size_spectra_model_lagged, main
= “Size spectrum slope model”) print(size_sprectra_plot)

#How good is the regression line fitted to the data points?
r_squared_THE_size_spectra_model_lagged_no_outliers <-
r.squaredGLMM(no_outliers_THE_size_spectra_model_lagged)

#Where R2m represent the proportion of variance explained by the fixed
effects #R2c represents the proportion of variance explained by both the
fixed and random effects

print(r_squared_THE_size_spectra_model_lagged_no_outliers)
```

```
#Calculating VIF
vif_no_outliers_THE_size_spectra_model_lagged <-
car::vif(no_outliers_THE_size_spectra_model_lagged)
print(vif_no_outliers_THE_size_spectra_model_lagged)

dev.off()


#Predict size spectra
predicted_values_size <- predict(no_outliers_THE_size_spectra_model_lagged,
newdata = lagged_data)

#Assign predicted size spectra slope values back to the original data
lagged_data$predicted_size_spectra_slope <- predicted_values_size


#Plot the size spectrum slope over temperature with line from model output
slope_size_spectra <- ggplot(lagged_data, aes(x = lagged_airtemp_june_aug,
y = size_spectra_slope_value, color = lake)) + geom_point(size = 1.5) +
geom_smooth(aes(y = predicted_size_spectra_slope), method = “lm”, se =
FALSE, color = “red”, linetype = “solid”) + labs(x = “Lagged air
temperature [°C]”, y = “Size spectrum slope (b)”) + theme_minimal() +
theme( panel.background = element_rect(fill = “white”), # White background
panel.border = element_rect(color = “white”, fill = NA, size = 0.7), #
White border axis.line = element_line(color = “black”), panel.grid.major =
element_blank(), # Remove major gridlines panel.grid.minor =
element_blank(), # Remove minor gridlines legend.title = element_blank(),
legend.text = element_text(size = 15), axis.title = element_text(size = 20)
) + geom_text(aes(label = paste(“R2c =”, 0.62, “, R2m =”, 0.21)), x =
max(lagged_datalagged_airtemp_june_aug), y =
min(lagged_datasize_spectra_slope_value), hjust = 2, vjust = -0.25, size =
6, color = “black”) print(slope_size_spectra)


#Calculate quantiles for qqline – the residuals
residuals <- resid(no_outliers_THE_size_spectra_model_lagged) qq_line_data
<- data.frame(Theoretical = qnorm(ppoints(length(residuals))), Sample =
sort(residuals))


#Plot 1 with qqline
qq_plot <- ggplot(data.frame(residuals =
resid(no_outliers_THE_size_spectra_model_lagged)), aes(sample = residuals))
+ geom_qq() + geom_abline(intercept = 0, slope = sd(residuals)) +
xlab(“Theoretical Quantiles”) + ylab(“Sample Quantiles”)

#Plot 2 is the Homogeneity of variances
size_sprectra_plot <- plot(no_outliers_THE_size_spectra_model_lagged)


#Combined plot side by side for residuals and homogeneity of variances
plot_grid(qq_plot, size_sprectra_plot, ncol = 2, labels = c(“(a)”, “(b)”))
```

Year-plots ——————————————-

```
#Function to calculate p-value for mean body size for each lake
calculate_p_value_length <- function(data) { lm_model <-
lm(mean_length_limits_cm ~ year, data = data) shapiro_test <-
shapiro.test(residuals(lm_model)) return(shapiro_test$p.value) }
```

```
#Calculate p-value for mean body size for each lake
p_values_length <- BEST_BIG_ONE %>% group_by(lake) %>%
summarize(p_values_length = calculate_p_value_length(cur_data_all()))

BEST_BIG_ONE <- left_join(BEST_BIG_ONE, p_values_length, by = “lake”)
```

```
#Plot mean body size over time, with dashed lines indicating not
significant and solid lines indicating significant
plot_length <- ggplot(BEST_BIG_ONE, aes(x = year, y =
mean_length_limits_cm, color = lake, group = lake)) + geom_point(size =
1.5) + geom_smooth(aes(linetype = ifelse(p_values_length < 0.05, “solid”,
“dashed”)), method = “lm”, se = FALSE, size = 0.7) + labs(x = “Year”, y =
“Mean length [cm]”) + scale_linetype_manual(values = c(“solid” = “solid”,
“dashed” = “dashed”)) + theme_minimal() + theme( panel.background =
element_rect(fill = “white”), # White background panel.border =
element_rect(color = “white”, fill = NA, size = 0.7), # White border
axis.line = element_line(color = “black”), panel.grid.major =
element_blank(), # Remove major gridlines panel.grid.minor =
element_blank(), # Remove minor gridlines legend.title = element_blank(),
axis.title = element_text(size = 14) ) print(plot_length)
```

```
#Funtion to calculate p-value for size spectra for each lake
calculate_p_value_slope <- function(data) { lm_model <-
lm(size_spectra_slope_value ~ year, data = data) shapiro_test <-
shapiro.test(residuals(lm_model)) return(shapiro_test$p.value) }
```

```
#Calculate p-value for size spectra for each lake
p_values_slope <- BEST_BIG_ONE %>% group_by(lake) %>%
summarize(p_values_slope = calculate_p_value_slope(cur_data_all()))

BEST_BIG_ONE <- left_join(BEST_BIG_ONE, p_values_slope, by = “lake”)
```

```
#Plot size spectra slope over year, with dashed lines indicating not
significant and solid lines indicating significant
plot_slope <- ggplot(BEST_BIG_ONE, aes(x = year, y =
size_spectra_slope_value, color = lake, group = lake)) + geom_point(size =
1.5) + geom_smooth(aes(linetype = ifelse(p_values_slope < 0.05, “solid”,
“dashed”)), method = “lm”, se = FALSE, size = 0.7) + labs(x = “Year”, y =
“Size spectrum slope”) + scale_linetype_manual(values = c(“solid” =
```

```
“solid”, “dashed” = “dashed”), name = NULL) + theme_minimal() + theme(
panel.background = element_rect(fill = “white”), # White background
panel.border = element_rect(color = “white”, fill = NA, size = 0.7), #
White border axis.line = element_line(color = “black”), panel.grid.major =
element_blank(), # Remove major gridlines panel.grid.minor =
element_blank(), # Remove minor gridlines legend.title = element_blank(),
axis.title = element_text(size = 14) ) print(plot_slope)
```

```
#Calculate slope for size spectra for each lake
slope_values <- BEST_BIG_ONE %>% group_by(lake) %>% summarize(slope_value =
coef(lm(size_spectra_slope_value ~ year, data = cur_data_all()))[2])
```

```
#Combine slope and p-values
slope_significance_table <- left_join(slope_values, p_values_slope, by =
“lake”)
```

```
#Adding a column indicating if the slope is significant or not
slope_significance_table$significant <-
slope_significance_table$p_values_slope < 0.05
```

```
#Calculate slope for mean body size for each lake
length_values <- BEST_BIG_ONE %>% group_by(lake) %>% summarize(length_value
= coef(lm(mean_length_limits_cm ~ year, data = cur_data_all()))[2])
```

```
#Combine slope for mean body size and p-values
length_significance_table <- left_join(length_values, p_values_length, by =
“lake”)
```

```
#Adding a column indicating if the slope is significant or not
length_significance_table$significant <-
length_significance_table$p_values_length < 0.05
```

Combined year-plot, mean body size and size spectra over time ——

```
#Create text annotations
text_a <- textGrob(“(a)”, x = 0.09, y = 0.95, just = c(“left”, “top”), gp =
gpar(fontsize = 14)) text_b <- textGrob(“(b)”, x = 0.09, y = 0.95, just =
c(“left”, “top”), gp = gpar(fontsize = 14))
```

```
#Combine text annotations with plots
plot_length_with_label <- arrangeGrob(text_a, plot_length +
theme(legend.position = “none”) + theme(axis.title.x = element_blank()),
ncol = 1, heights = c(0.1, 1))
```

```
plot_slope_with_label <- arrangeGrob(text_b, plot_slope +
theme(legend.position = “none”), ncol = 1, heights = c(0.1, 1))
```

```
#Combine plots, text annotations, and legend
grid.arrange(plot_length_with_label, plot_slope_with_label, ncol = 1,
heights = c(1, 0.2, 1))
```

```
legend_length <- cowplot::get_legend(plot_length + theme(legend.text =
element_text(size = 14)))
```

```
#Combine plots and text annotations
plots <- plot_grid(plot_length_with_label, plot_slope_with_label, ncol = 1)

#Create a new plot with the legend
combined_plot <- plot_grid(plots, legend_length, rel_widths = c(1, 0.2))

#Print the combined plot, mean body size and size spectra over time
print(combined_plot)
```