

SALINIZATION AND WARMING EFFECTS ON ZOOPLANKTON
COMMUNITY IN MEDITERRANEAN SHALLOW LAKES: A MESOCOSM
EXPERIMENT

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MESOCOSM EXPERIMENT**

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ABSTRACT

SALINIZATION AND WARMING EFFECTS ON ZOOPLANKTON COMMUNITY IN MEDITERRANEAN SHALLOW LAKES: A MESOCOSM EXPERIMENT

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Freshwater ecosystems in Mediterranean climate zones are increasingly impacted by climate change. Altered precipitation patterns, together with elevated evaporation rates, reduce lake water volumes and consequently increase salinity. This increase can significantly alter aquatic community structure. While previous studies have often addressed the effects of warming or salinity separately, the combined effects of these stressors remain poorly understood, and research on hypersaline lakes is still limited. This study examined the responses of zooplankton communities to the combined effects of salinity and warming.

A mesocosm experiment was conducted at the METU IMS Mersin, Türkiye, between September and November 2023, applying two salinity treatments (4 g/L and 40 g/L) and two temperature conditions (ambient temperature and ambient +4.5°C warming) to simulate potential future climate scenarios. The results revealed a pronounced shift in community composition between the salinity treatments. At 4 g/L, zooplankton communities were dominated by large-bodied taxa. In contrast, at 40 g/L salinity, these larger taxa were largely eliminated and replaced by halotolerant rotifers, primarily *Brachionus plicatilis*. PERMANOVA results indicated that warming had no significant effect on biomass, abundance, and composition of

zooplankton. GAM analyses further indicated that Shannon diversity and evenness were higher at 4 g/L, while high salinity resulted in a rotifer-dominated community. Notably, warming exacerbated the reduction in diversity specifically at 40 g/L.

Overall, these findings emphasize that increasing salinization, particularly in combination with warming, can alter zooplankton community structure in Mediterranean lakes, with potential cascading effects on trophic interactions, ecosystem stability, and freshwater management strategies.

Keywords: Climate Change, Freshwater, Salinization, Warming, Zooplankton, Mediterranean Region, Mesocosm

ÖZ

AKDENİZ SIĞ GÖLLERİNDE TUZLANMA VE ISINMANIN ZOOPLANKTON KOMÜNİTESİ ÜZERİNE ETKİLERİ: BİR MEZOKOZM DENEYİ

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Akdeniz iklim kuşağındaki tatlı su ekosistemleri iklim değişikliğinden giderek daha fazla etkilenmektedir. Değişen yağış rejimleri ve artan buharlaşma oranları, göl su hacimlerini azaltarak tuzluluğun artmasına neden olur. Bu artış, sucul topluluk yapısını önemli ölçüde değiştirebilir. Önceki çalışmalar genellikle ısınma veya tuzluluğun etkilerini ayrı ayrı ele almış olsa da, bu stresörlerin birleşik etkileri hâlâ yeterince anlaşılmamıştır ve hipersalin göller üzerine yapılan araştırmalar sınırlıdır. Bu çalışma, zooplankton topluluklarının tuzluluk ve ısınmanın birleşik etkilerine verdiği yanıtları incelemiştir.

Eylül–Kasım 2023 tarihleri arasında ODTÜ DBE Mersin, Türkiye’de bir mezokozm deneyi yürütülmüş; iki tuzluluk düzeyi (4 g/L ve 40 g/L) ile iki sıcaklık koşulu (ortam sıcaklığı ve ortam +4.5°C) uygulanarak olası gelecekteki iklim senaryoları simüle edilmiştir. Sonuçlar, tuzluluk düzeyleri arasında topluluk yapısının belirgin şekilde değiştiğini göstermiştir. 4 g/L’de zooplankton toplulukları büyük gövdeli taksonlar tarafından baskınken, 40 g/L’de bu büyük türler büyük ölçüde ortadan kalkmış ve yerlerini başta *Brachionus plicatilis* olmak üzere halotolerant rotiferler almıştır. PERMANOVA sonuçları, ısınmanın zooplankton biyokütlesi ve bolluğu üzerinde anlamlı bir etkisi olmadığını göstermiştir. GAM analizleri ise Shannon çeşitliliği değerlerinin 4 g/L’de daha yüksek olduğunu, yüksek tuzlulukta ise rotifer-baskın bir

topluluğun oluřtuđunu ortaya koymuřtur. Dikkat çekici olarak, ısınma etkisi özellikle 40 g/L'de çeřitlilikteki azalmayı daha da řiddetlendirmiřtir.

Genel olarak, bu bulgular artan tuzluluđun özellikle ısınma ile birleřtiđinde Akdeniz bölgesi göllerinde zooplankton topluluk yapısını deđiřtirebileceđini göstermekte; bunun da trofik etkileřimler, ekosistem kararlılıđı ve tatlı su yönetim stratejileri üzerinde potansiyel zincirleme etkileri olabileceđine iřaret etmektedir.

Anahtar Kelimeler: İklim deđiřikliđi, Tatlı su, Tuzlanma, Isınma, Zooplankton, Akdeniz Bölgesi, Mezokozm

Açtıđın yolda, gösterdiđin hedefe...

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TABLE OF CONTENTS

ABSTRACT.....	v
ÖZ	vii
ACKNOWLEDGMENTS	x
TABLE OF CONTENTS.....	xi
1. İçindekiler	xi
LIST OF TABLES	xiii
LIST OF FIGURES	xiv
CHAPTERS	
1 INTRODUCTION	1
2 MATERIALS & METHODS	13
2. 1. Study Site	13
2. 2. Experimental Set-up.....	14
2. 3. Mesocosm Ecosystems and Inoculation of Aquatic Communities.....	16
2. 4. Sampling and Analyses.....	17
2. 5. Zooplankton Sampling and Identification.....	19
2. 6. Data Analysis	20
3 RESULTS	23
3. 1. Physico-chemical Response.....	23
3.2 Zooplankton Community Analysis	35
4 DISCUSSION	51

4.1. Limitations.....	60
5 CONCLUSION	63
REFERENCES	65

LIST OF TABLES

TABLE

Table 1. Experiment treatments and randomly assigned mesocosms.....	15
Table 2. Zooplankton species observed throughout the experiment.....	35
Table 3. Table of species contributing most to abundances according to SIMPER analysis.....	37
Table 4. Pairwise PERMANOVA results showing the effects of salinity, temperature, and their combined impact on zooplankton total biomass, average body length, and abundance across treatments. Stars indicate statistically significant differences, while the position of the arrows (left or right of the significance symbol) denotes which treatment exhibited the higher value. Blue arrows denote directional, mean-driven treatment effects, whereas pink arrows indicate variance-driven effects resulting from increased among-replicate variability rather than consistent shifts in mean values.	49

LIST OF FIGURES

FIGURE

Figure 1. Illustration of how increased temperature leads to higher evaporation rates, resulting in decreased water volume and increased salinization in aquatic systems.	5
Figure 2. General body structures of three major zooplankton groups: (a) Rotifera, (b) Cladocera, and (c) Copepoda (Thackeray & Beisner, 2024).	8
Figure 3. Study site of the mesocosm experiment (Mersin, southern Türkiye), located in the Mediterranean climate zone.	13
Figure 4. Aerial photo of the mesocosm facility at the Institute of Marine Sciences (Photo by Korhan Özkan, 2023).	14
Figure 5. Schematic representation of treatments used in the experiment.	15
Figure 6. Schematic representation of the interior and exterior of mesocosm tanks (Billah et al., 2024).	16
Figure 7. Materials and equipment used for zooplankton sampling in the mesocosm experiment.	20
Figure 8. Temperature changes over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.	23
Figure 9 . Salinity changes over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.	24
Figure 10. Secchi depth over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.	25
Figure 11. Chlorophyll-a (Chl-a) values over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.	26
Figure 12. Total Suspended Solid (TSS) values over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.	27
Figure 13 Dissolved oxygen (DO) values over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.	28
Figure 14 Total phosphate (TP) concentrations over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.	29

Figure 15. Total nitrogen (TN) concentrations over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.	30
Figure 16 . NO ₃ concentrations over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.	31
Figure 17. Soluble Reactive Phosphorus (SRP) concentrations over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.	32
Figure 18. Spearman correlations among physicochemical parameters.	33
Figure 19. PCA plot of environmental data, triangles for warming, circles for no warming, and colors indicating salinity: blue = 4 g/L, red = 40 g/L.	34
Figure 20. Graph illustrating the relative contributions of major zooplankton taxa to overall community abundance across treatments.	36
Figure 21. Total zooplankton abundance over time graph. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L) Error bars show standard errors.	38
Figure 22. NMDS plot of zooplankton community composition (abundance) based on Bray–Curtis dissimilarities (Stress = 0.124).	39
Figure 23. Graph showing total zooplankton biomass composition by major taxonomic groups.	40
Figure 24. NMDS plot of community structure based on species-specific biomass (stress = 0.098).	41
Figure 25. Total zooplankton biomass over time graph. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L).	42
Figure 26. Graph of indicator species per treatment.	43
Figure 27. Partial effect plots and model diagnostics from the GAM.	44
Figure 28. Zooplankton Shannon diversity over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). .	45
Figure 29. Zooplankton richness over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L).	46
Figure 30. Changes in community-weighted mean (CWM) body length of Cladocera and Rotifera groups. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L).	47
Figure 31. Body length of the most abundant genus. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). .	48
Figure 32. NMDS plot showing the relationship between environmental parameters and species composition.	49
Figure 33. Representation of the direct and indirect impacts of salinity on zooplankton communities.	56

CHAPTER 1

INTRODUCTION

Climate change, combined with human activities such as overexploitation and socioeconomic pressures, leads to multiple environmental stressors. These include rising temperatures, increased atmospheric CO₂ levels, and more frequent and intense droughts, as well as changes in precipitation patterns 12/25/2025 1:38:00 PM. In addition to the expected effects of changes in temperature and precipitation, an increase in extreme weather events such as heatwaves, storms, and heavy rainfall may also affect ecosystems (Calvin et al., 2023; Y. Sun et al., 2025; Woolway et al., 2021). In particular, heatwaves can cause shallow lakes to become temporarily stratified, which increases internal phosphorus loading and may lead to eutrophication (Wilhelm & Adrian, 2008; Woolway et al., 2021). On the other hand, severe drought can cause lake water levels to drop, resulting in increased salt and nutrient concentrations and a decline in water quality (Jeppesen et al., 2021). Long-term droughts may even alter community dynamics and food-web structure in aquatic ecosystems.(Vargas et al., 2024).

Freshwater habitats, comprising only 0.8% of the Earth's surface and 0.01% of all water reserves, represent a small fraction of global water resources. Despite their limited extent, freshwater ecosystems support over 10,000 fish species and are characterized by high levels of endemism and biodiversity. Nearly one-third of all vertebrate species inhabit freshwater when amphibians, aquatic reptiles, and mammals are included alongside freshwater fish (Dudgeon et al., 2006). Nevertheless, freshwater systems are particularly vulnerable to climate change and human exploitation, partly due to their relative isolation and intensive use for irrigation and drinking water (Jeppesen et al., 2014; Woodward et al., 2010). This vulnerability is evident from the decline of populations of several taxonomic and

functional groups of freshwater organisms, which have decreased by more than 80% since 1975, with an estimated annual average rate of 4% (Meerhoff & Beklioglu, 2024).

Shallow lakes, as a type of freshwater ecosystem, are the most widespread form of freshwater habitats. Although referred to as “shallow”, they are taxonomically and functionally diverse, particularly in terms of aquatic vegetation (Scheffer, 2004). These ecosystems host abundant in terms of plants, amphibians, invertebrates, and water birds due to their high vegetative abundance (Scheffer et al., 2006). Because the water column mixes frequently, shallow lakes are generally classified as polymictic. While definitions of their depth vary in the literature, they are typically considered to be less than three meters deep (Scheffer, 2004). The high density of organisms within a limited water volume results in complex biological interactions, including competition among species, which are critical for maintaining water quality, biodiversity, and carbon cycling (Meerhoff & Beklioglu, 2024). Like other freshwater systems, shallow lakes are sensitive ecosystems, and their protection through restoration programs is essential (Meerhoff & de los Ángeles González-Sagrario, 2022). Increasing anthropogenic pressures and changes in water column dynamics, such as the emergence of thermal stratification, can lead to unpredictable declines in water quality. Elevated nutrient levels, for instance, may trigger rapid phytoplankton blooms (Velthuis et al., 2017). These blooms may form a surface layer that limits sunlight penetration to deeper water. Furthermore, as phytoplankton respire and decompose, oxygen concentrations in the water decrease, adversely affecting aquatic organisms and overall ecosystem functioning (Boyd, 2020; Wetzel, 2001). Shallow lakes and ponds in various regions are experiencing salinization or drying due to global climate change and rising water demand, especially in arid and semi-arid areas (Bruce et al., 2012; Yilmaz et al., 2021). These changes, combined with eutrophication, are expected to accelerate biodiversity loss and increase the carbon footprint of these ecosystems (Nazari-Sharabian et al., 2018). The growing demand for food to support a rising population, combined with intensified irrigation practices, has further threatened shallow lake ecosystems. This is evident in the

Konya Closed Basin (Yılmaz et al., 2021), where these activities have contributed to a significant reduction in lake and wetland surface areas. Consequently, 18 of the 62 historic breeding species of waterbirds in the basin have already disappeared, and three internationally vulnerable species are now at risk of extinction (Çolak et al., 2022).

The Mediterranean semiarid climate zone is a region characterized by low annual precipitation and high evaporation (Coppens et al., 2020). Consequently, this region is highly susceptible to drought and is extensively used for irrigation (Kurunç & Doganay, 2022). According to a recent global circulation model and taking the 1960-1970 period as a reference it is estimated that there will be an increase of at least to 2C ° degrees in the average spring and summer temperatures and a total annual decrease of 10 percent in precipitation between 2070 and 2100 in Türkiye (Cos et al., 2022; Önol & Unal, 2014). Also, according to the Intergovernmental Panel on Climate Change (IPCC) 2023 report, global surface temperatures are projected to increase significantly ranging from 1.1°C to 6.4°C by the end of this century (Calvin et al., 2023). Shallow lakes in Mediterranean semi-arid regions are particularly susceptible to drought because of low rainfall combined with high evaporation rates. Increasing temperatures exacerbate this trend, accelerating water loss. As water evaporates from lakes, the concentration of remaining salts increases, leading to salinization, which can affect many aquatic species. Furthermore, the combined effects of salinization and rising temperatures can have a more pronounced impact on aquatic ecosystems (von Weissenberg et al., 2022; R. H. Walker et al., 2020).

Temperature is an environmental factor that influences biological and biochemical processes in freshwater systems, affecting species diversity, distribution, reproduction, growth rates, food web interactions, and greenhouse gas emissions (Maberly et al., 2020; Pal et al., 2014). Elevated temperatures can promote cyanobacterial blooms, which are low quality food sources, thereby reducing the efficiency of energy transfer from phytoplankton to zooplankton and making energy flow through the food web less effective (Mooij et al., 2007). With increasing temperature, metabolic rates rise, leading to higher energy demands. To optimize

energy use, species may reduce their body size, which can have multiple ecological consequences. Smaller body sizes in zooplankton may weaken energy transfer to higher trophic levels, alter food web dynamics, and simultaneously affect fecundity, population growth, and competitive interactions (Atkinson, 1995; Daufresne et al., 2009). Beyond these biological impacts, rising temperatures alter thermal regimes and increase evaporation rates, driving changes in physicochemical parameters that may affect aquatic biodiversity (Valido et al., 2020). Organisms in arid and semiarid aquatic environments develop a variety of adaptation mechanisms to cope with these combined biological and physical changes, including switching to anaerobic respiration under low-oxygen conditions, entering dormancy during dry periods until favorable conditions return, and producing resistant eggs (Arenas-Sánchez et al., 2019; Storey & Quinn, 2008). Despite these adaptations, rising temperatures can still have serious effects on ecosystems by disrupting population dynamics, interspecies interactions, and ecosystem functions through alterations in species physiological processes (Prakash, 2021; Traill et al., 2010).

Salinization is becoming an increasingly important global water quality issue in the world (Cañedo-Argüelles, 2020; Kirtel et al., 2018; Williams, 2001). Climate change-related warming alters evaporation and precipitation patterns, and when evaporation exceeds precipitation, water bodies begin to dry out as water loss surpasses water input. As a result, salinity increases as salts concentrate in the reduced volume of water (Kaushal et al., 2021). Higher salinity in freshwater ecosystems affects many organisms in the food chain such as phytoplankton, zooplankton, fish, and insect larvae because the salt concentration in their bodies must stay in balance with their surroundings (Ersoy et al., 2022; Hintz et al., 2018; Jeppesen et al., 2014). Increased salinity creates physiological stress for many freshwater species, disrupting osmoregulation and leading to reduced survival and reproduction rates. As a result, more sensitive species disappear, and overall community structure shifts, often favoring a few salt-tolerant taxa (Ersoy et al., 2022; Hébert et al., 2023; Hintz et al., 2019; Huber et al., 2023; tavşanoğlu et al., 2015).

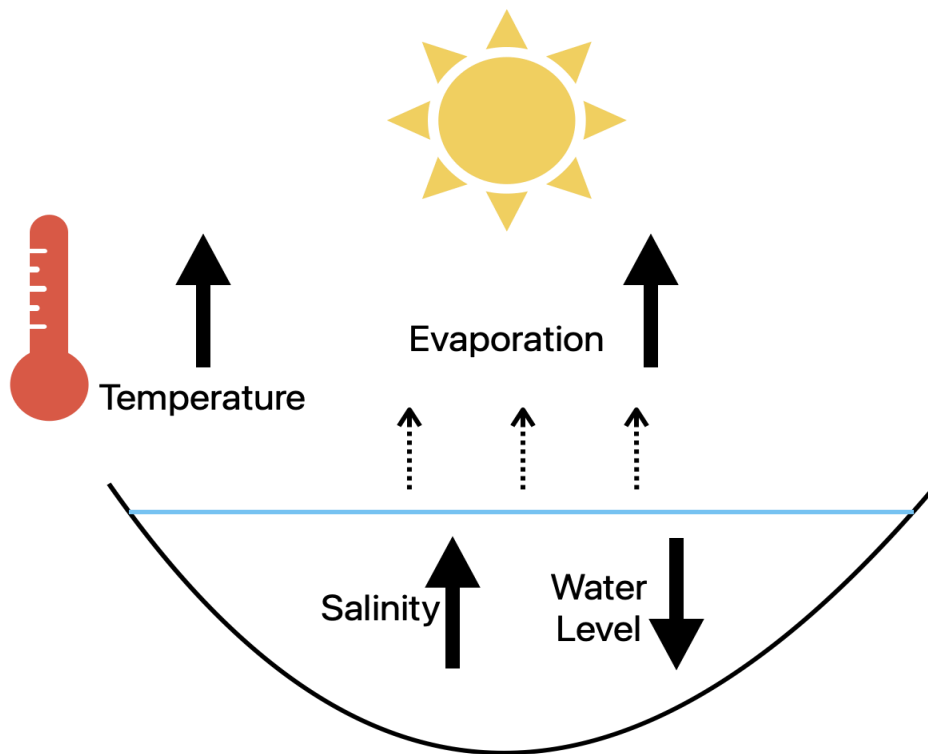


Figure 1. Illustration of how increased temperature leads to higher evaporation rates, resulting in decreased water volume and increased salinization in aquatic systems.

Plankton are microscopic organisms that drift in aquatic environments due to their limited swimming ability. They are broadly classified into two main groups as phytoplankton and zooplankton. Phytoplankton, which are unicellular photosynthetic organisms, serve as the primary producers in aquatic food webs, contributing approximately 45% of the global annual primary production (Brierley, 2017). These organisms form the foundational food source for zooplankton, which in turn provide energy to higher trophic levels, including commercially important fish species. Beyond their ecological role, phytoplankton play a vital part in the global biogeochemical cycles by sequestering atmospheric carbon dioxide and transporting it to deeper waters, thereby mitigating carbon emissions in the atmosphere (Brierley, 2017; Reynolds, 2006).

Zooplankton are primary consumers in aquatic food webs. They receive energy from primary producers and pass it on to higher consumers, thereby facilitating the flow of energy from the base to the top of the food chain (Dodson & Frey, 2001; Wetzel, 2001). Zooplankton exhibit diverse feeding strategies, including herbivory, carnivory, and omnivory. This nutritional variability can differ significantly across taxonomic groups and species (Dodds, 2010). They contribute to nutrient remineralization, thereby affecting algae and microbial populations, and can also directly reduce these populations through grazing (Hessen et al., 1995; Jeppesen et al., 2003; Schriver et al., 1995). The composition and dynamics of zooplankton communities are influenced by various environmental factors such as nutrient availability, water levels, and habitat structure (Badsı et al., 2010). The growth and reproduction of zooplankton are closely linked to the quality of their food; for example, global warming can increase water stratification, reducing vertical nutrient mixing and limiting the availability of high-quality diatoms (Winder & Schindler, 2004). Consequently, zooplankton may shift to less nutritious phytoplankton species. (Hessen et al., 2004; Gulati & DeMott, 1997). Due to their high abundance, short life cycles, diverse species composition, and varying tolerance to environmental stressors, zooplankton are widely regarded as valuable bioindicators for monitoring physical, chemical, and biological changes in aquatic environments (Alcaraz & Calbet, 2003; Wetzel, 2001). The main groups within zooplankton include Rotifera, Copepoda, and Cladocera.

Cladocera can inhabit various freshwater environments such as lakes, ponds, rivers, and wetlands. Most species are small, typically measuring between 0.2 and 0.3 mm in length. Many members of this group are filter feeders, consuming phytoplankton, bacteria, and detritus however, some genera, such as *Leptodora*, *Polyphemus*, and *Pseudochydorus*, as well as members of the Onychopoda and Haplopoda groups, are predators (Williams, 2001). Cladocerans play a crucial role in shaping microbial loops in freshwater ecosystems by grazing on bacteria. Characteristic features of Cladocerans include a large compound eye (in some species, a second small simple eye, or ocellus, may be present) and five pairs of lobed thoracic legs. The head have

one pair each of antennae, mandibles, and maxillae. Most Cladocerans reproduce through parthenogenesis, and after several generations, they may switch to gamogenetic reproduction. (Bledzki & Rybak, 2016; Dodson & Frey, 2001; Wetzel, 2001).

Copepoda is a subclass within the subphylum Crustacea, and its members are widely distributed across nearly all aquatic ecosystems however they are mainly common in marine system rather than freshwater. Compared to Cladocerans, copepods have a distinctly segmented body structure and head segment is covered by a carapace. Reproduction in copepods is sexual, with separate sexes. The copepod life cycle includes six nauplius stages (N1–N6), followed by six copepodite stages (C1–C6), the last of which is the adult form. In freshwater ecosystems, copepods play a significant role in controlling prey populations. At the same time, they serve as prey for other copepods and various fish species (Wetzel, 2001; Williamson & Reid, 2001).

Rotifers are generally smaller in size compared to Cladocera and Copepoda groups, typically ranging from 50 to 2000 μm in length. They are found in many freshwater habitats and show a high diversity of species. Most rotifer species are transparent and very small. These traits reduce their visibility to fish predators, offering some survival advantage. However, their small body size also makes them more vulnerable to invertebrate predators (Wallace et al., 2019). Rotifers have a structure called the corona on their head, which helps them swim, feed, and capture small algae, detrital particles, and bacteria. Compared to Cladocera and Copepoda, rotifers are generally weaker competitors. Reproductive strategies vary widely among rotifer species. Most species in the class Monogononta exhibit cyclical parthenogenesis, where asexual reproduction is dominant, but sexual reproduction also occurs under certain conditions (Thorp & Rogers, 2019; Wallace et al., 2019).

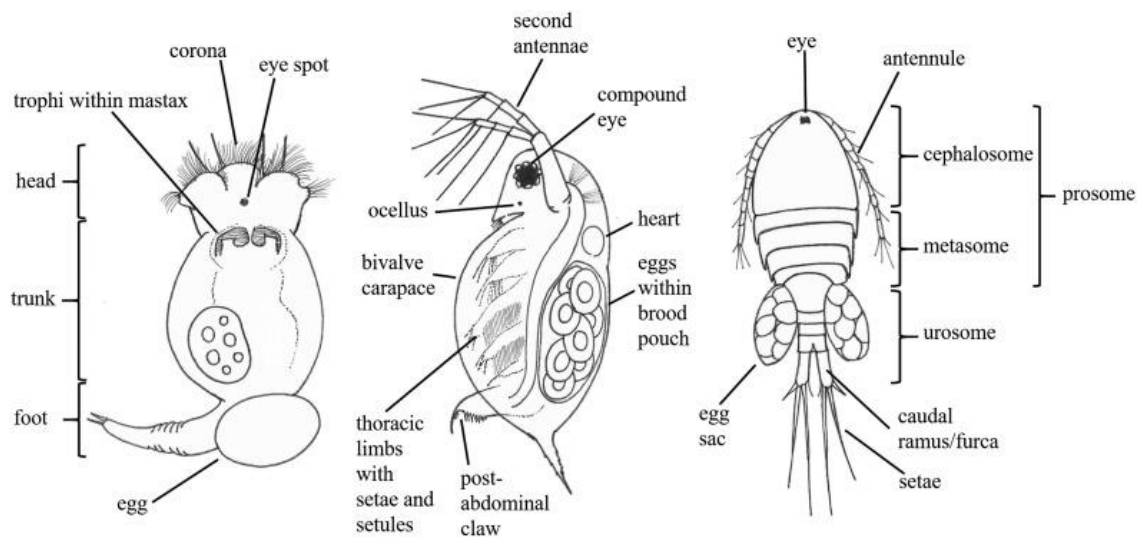


Figure 2. General body structures of three major zooplankton groups: (a) Rotifera, (b) Cladocera, and (c) Copepoda (Thackeray & Beisner, 2024).

Many ecosystems face threats from global changes such as warming and salinization. Although scientific research and experiments are essential to protect these ecosystems, predicting climate change impacts remains difficult because ecosystems vary widely in terms of water cycles and chemical processes (Boyle & Fairchild, 1997; Odum, 1984). Experimental ecology uses controlled experiments to better understand these complex ecological issues. Larger experiments tend to be more effective as ecosystems become more complex, and mesocosm studies, in particular, mimic natural ecosystems and help analyze biological interactions (Özkan et al., 2023).

Many zooplankton groups and taxa are dependent on certain salinity thresholds, which determine their tolerance ranges and strongly influence community composition and abundance in aquatic habitats (Schallenberg et al., 2003). As salinity increases, species with high salt tolerance typically become dominant over those with low tolerance, leading to the replacement of large and efficient filter feeders (e.g., cladocerans and copepods) by smaller and less efficient groups such as rotifers (Ersoy et al., 2022; Hébert et al., 2023). These shifts can weaken grazing pressure on phytoplankton and may ultimately promote algal blooms, thereby

affecting overall water quality. Considering the interconnected roles of multiple environmental drivers, more research is needed to fully understand the ecosystem-level consequences of salinization (Hébert et al., 2023).

Several studies have further demonstrated that increasing salinity negatively affects zooplankton communities through both direct physiological intolerance and indirect ecological pathways. For example, (Hall & Lewandowska, 2022). reported that elevated salinity reduces zooplankton abundance due to osmotic stress while also modifying community structure indirectly by decreasing phytoplankton biomass through oxidative stress, leading to food limitation. Similarly, (Gutierrez et al., 2018) found that rising salinity decreases species richness, specific diversity, functional diversity, body size, and biomass primarily due to physiological constraints resulting in simplified and more vulnerable trophic structures. These findings suggest that biodiversity and ecosystem functioning in arid and semi-arid regions may further deteriorate under future climate change scenarios.

Several studies have demonstrated that increasing salinity negatively affects zooplankton communities through both direct physiological intolerance and indirect ecological pathways. For example, Hall & Lewandowska (2022) reported that elevated salinity reduces zooplankton abundance due to osmotic stress while also indirectly modifying community structure by decreasing phytoplankton biomass through oxidative stress, leading to food limitation. Similarly, Gutierrez et al., (2018) found that rising salinity decreases species richness, specific diversity, functional diversity, body size, and biomass primarily due to physiological constraints, resulting in simplified and more vulnerable trophic structures. Supporting these findings, Lin et al., (2017) investigated 45 lakes along an altitudinal temperature gradient on the Tibetan Plateau and found that salinity promoted saline-adapted species, increased the zooplankton-to-phytoplankton biomass ratio, and reduced zooplankton species richness, especially among copepods and small cladocerans. Furthermore, in systems dominated by large herbivorous zooplankton, higher temperatures amplified the zooplankton-to-phytoplankton biomass ratio, indicating interactive effects between temperature and salinity.

In addition to salinity, warming has also been identified as a key driver shaping zooplankton communities. Altındağ et al., (2025) showed that in Türkiye's freshwater littoral zones, global warming favored small zooplankton species, particularly rotifers, which are opportunistic under extreme conditions. This shift toward rotifer dominance reduced overall body sizes within the zooplankton communities and altered community composition. Similarly, Strecker et al., (2004) observed in fishless alpine ponds that a warming treatment (3.68°C increase) in mesocosms suppressed total zooplankton biomass over a 50-day experiment, largely due to declines in large cladocerans (*Daphnia pulex*), while rotifer abundance increased. These results align with observations in Türkiye, indicating consistent shifts toward smaller, opportunistic species under elevated temperatures.

However, warming effects can also be subtle and species-specific. Mckee et al., (2002) found in a 48-replicate microcosm experiment that while cladoceran diversity and overall abundance were not significantly affected by warming, community evenness increased. In *Simocephalus vetulus*, adult body size declined under warming, copepod populations decreased in size, and ostracod populations increased, highlighting nuanced, species-specific responses.

Recent experimental studies examining heatwave events further emphasize the complexity of zooplankton responses to sudden temperature increases. Sun & Arnott (2022) conducted a mesocosm experiment testing the combined effects of elevated salinity and heatwaves. While each stressor alone impaired zooplankton communities, their combined effect was antagonistic because salinity acted as the dominant stressor and masked the impact of the heatwave. When stressors were applied sequentially, communities retained a “memory” of prior exposure, with zooplankton previously exposed to salinity better able to cope with a subsequent heatwave than those exposed to temperature stress alone (Sun & Arnott, 2022). These findings underline that both the magnitude and timing of stressors are critical in determining community responses.

Despite these advances, a significant knowledge gap remains regarding how zooplankton communities in Mediterranean-climate lakes respond to the combined

effects of salinity and warming. Mediterranean lakes experience strong seasonal fluctuations, characterized by high summer temperatures and increasing salinity driven by evaporation. Therefore, in this study, we investigated how zooplankton communities from lakes in the Mediterranean region respond to the combined impacts of elevated temperature and salinity, with the aim of improving understanding of stressor interactions under climate change.

In this study, a mesocosm facility located in METU-IMS was used to simulate shallow lakes in a dry Mediterranean climate to investigate how zooplankton communities respond to salinization and warming. Two contrasting salinity levels (4 g/L and 40 g/L) were applied, together with two temperature regimes (ambient and 4.5 °C above ambient), to examine their combined effects. We hypothesize that large zooplankton groups, such as cladocerans and copepods, will decline under the combined stress of warming and salinity, while smaller groups, such as rotifers, will become more dominant. These shifts are expected to alter community structure by favoring species with higher tolerance to environmental stress.

We also hypothesize that zooplankton richness, diversity, abundance, and biomass will decrease under high salinity (40 g/L), as only halotolerant species can persist. In contrast, low salinity (4 g/L) is expected to support a more diverse and abundant community.

Lastly, we hypothesize that the combined effects of warming and salinization will result in smaller zooplankton body sizes compared to no-warming treatments, due to increased metabolic rates and accelerated development at higher temperatures. This reduction in body size may decrease the efficiency of energy transfer to higher trophic levels and ultimately alter food web structure.

Understanding the dynamics of zooplankton communities under varying salinity and temperature conditions is essential for assessing the combined impacts of multiple environmental stressors. Such investigations offer valuable insights into ecosystem responses to climate change and anthropogenic pressures, ultimately contributing to the development of more effective and sustainable management strategies for aquatic ecosystems.

CHAPTER 2

MATERIALS & METHODS

2. 1. Study Site

The mesocosm experiment was conducted in Mersin, on the campus of the Middle East Technical University (METU) Institute of Marine Sciences (IMS) (36°33'52.18"N, 34°15'14.50"E). Mersin is a coastal city in southern Türkiye, characterized by a hot and dry Mediterranean climate (Köppen-Geiger classification Csa), with an annual mean temperature of 19.6 °C. The experiment lasted four months from September to December 2023. Mesocosm set-up aimed to simulate shallow lake conditions and study how two temperature scenarios (ambient temperature and continuous warming of +4.5 C) and two salinity levels (4 and 40 g/L) (4 replicate tanks for each treatment) affecting zooplankton communities.



Figure 3. Study site of the mesocosm experiment (Mersin, southern Türkiye), located in the Mediterranean climate zone.



Figure 4. Aerial photo of the mesocosm facility at the Institute of Marine Sciences (Photo by Korhan Özkan, 2023).

2. 2. Experimental Set-up

16 mesocosms were used in the experiment, each with a diameter of 2 m, a height of 1.8 m and a volume of 5 m³. High-density polyethylene (HDPE) material was used to due to the resistance to high salinities and UV exposure. To minimize heat exchange, the mesocosm were buried at 1 m depth and exposed walls were insulated. Aquarium wave makers (5 watts) were used to prevent stratification and to circulate the water column in each mesocosm. Mesocosm were equipped with Pyroscience oxygen sensors (APHOX-S-O2) and temperature loggers in order to continuous measurements of oxygen and temperature values. Glass insulated heaters (3–4 kW each) were placed in half of the mesocosms. These mesocosms were randomly selected and heated using unheated reference mesocosms to induce dynamic warming. All the mesocosms were equipped with a microprocessor-based (Arduino Nano) controller, temperature sensors and a logging system. Based on real-time measurements from the reference (no-warming) mesocosms, the microprocessor in the warmed mesocosms automatically turned on or off the heating elements to maintain a desired temperature increase. Warming was initiated one week after the

start of the experiment, with gradual daily temperature increases of +0.64 °C. This cumulative increase continued for seven days, reaching a total of +4.5 °C by the end of the first week of the experiment.

Table 1. Experiment treatments and randomly assigned mesocosms.

Treatments	Mesocosm #
Ambient temperature & 4 g/L	4, 5, 12, 15
Ambient temperature & 40 g/L	1, 7, 9, 16
+4.5 °C Warming & 4 g/L	6, 8, 10, 11
+4.5 °C Warming & 40 g/L	2, 3, 13, 14

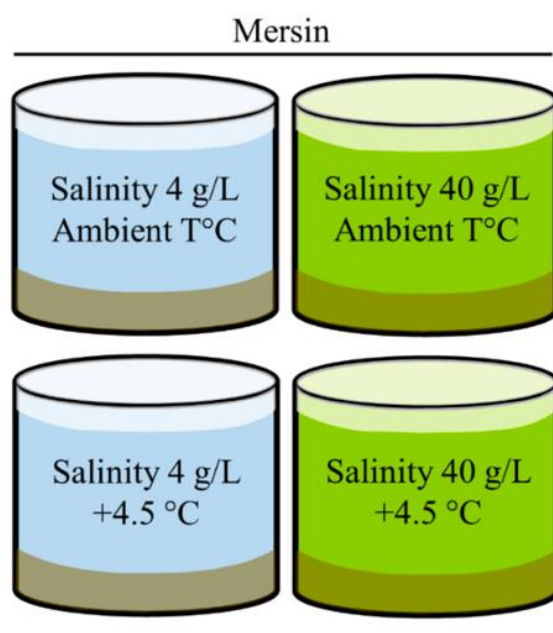


Figure 5. Schematic representation of treatments used in the experiment.

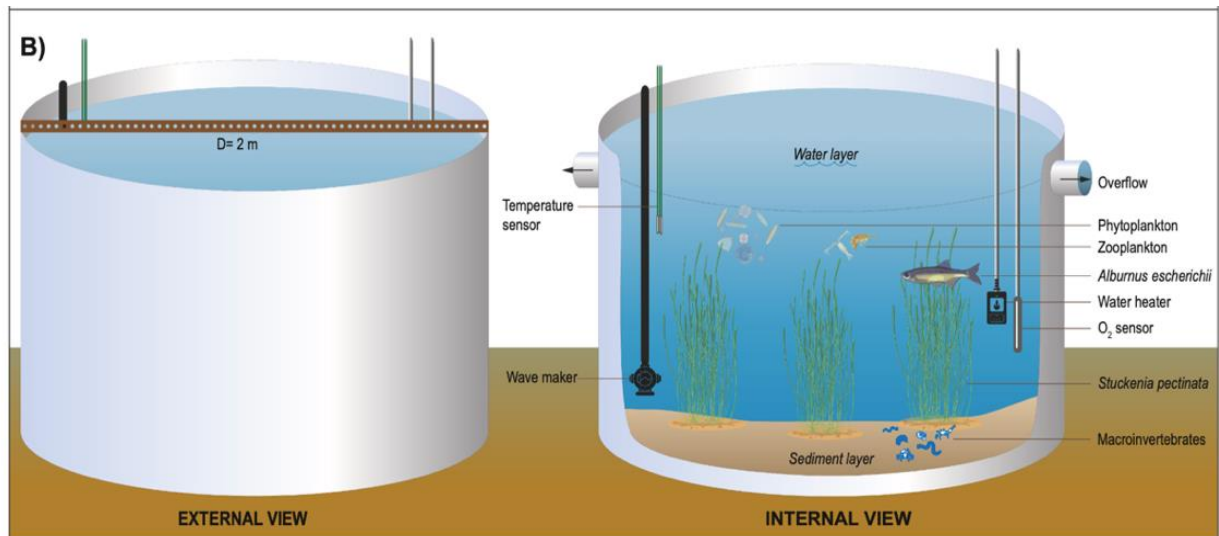


Figure 6. Schematic representation of the interior and exterior of mesocosm tanks (Billah et al., 2024).

2. 3. Mesocosm Ecosystems and Inoculation of Aquatic Communities

Each mesocosm contained 30 cm of sediment to replicate the realistic sediment biogeochemistry and to provide an important environment where zooplankton can remain dormant under harsh conditions (Gyllström & Hansson, 2004). To prepare the sediment, an equal mix of silicate sand and natural lake sediment was taken from Lake Uyuz (salinity 1.64 g/L) and Lake Kozanlı (salinity 1.0 g/L) in the construction of tanks 2 year prior to the current experiment. The prepared sediment evenly distributed across the mesocosms after being carefully mixed. All mesocosms were filled with groundwater (1.2 m water column height) and to compensate for water loss due to evaporation, groundwater was added every two weeks to all mesocosm. NaCl and Na₂ SO₄ are added to modify the salinity levels (with a ratio of 2.69 g L⁻¹ SO₄ to 35 g L⁻¹ salinity). Also, since the mesocosms are closed systems additional nutrients, including phosphates, nitrate and ammonia, were added weekly to compensate for nutrient losses. To simulate eutrophic conditions in line with the Trophic State Index for Lakes (Carlson, 1977), we applied nutrient additions weekly to maintain a TN:TP ratio of 20:1. Each mesocosm received 5.06 g of calcium nitrate

tetrahydrate ($\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$), 2.29 g of ammonium chloride (NH_4Cl), and 0.17 g of sodium dihydrogen phosphate dihydrate ($\text{Na}_2\text{H}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$).

The submerged macrophytes *Stuckenia pectinata* (L.) Börner, were collected from five coastal lagoons in the Göksu Delta region of Silifke and inoculated each mesocosm (around eight clusters). To standardize the initial conditions across all mesocosms, the macrophytes were trimmed two weeks before the experiment to reach a PVI of %50. 4 individuals of *Alburnus escherichii* Steindachner, 1897- a native Anatolian fish species tolerant to both eutrophic conditions and salinity- were collected from the Üçbaşlar pond, Ankara and added into the 4 g/L tanks when the target salinity was reached. Fish was not added to 40 g/L tanks because it is known that *A. escherichii* tolerate salinity levels between 12–17 g/L. Fish mortality was monitored daily in the mesocosm. In the event of a fish mortality, the dead fish was removed and replaced with a new one from the stock fish tank.

Natural plankton communities (such as bacteria, ciliates, phytoplankton, and zooplankton) and sediment samples were collected from five shallow coastal lakes and ponds with varying salinity levels (8-36 g/L) in the Göksu River Delta (Mersin) and subsequently inoculated into mesocosms. Plankton was gathered using nets with mesh sizes of 20 μm and 140 μm , while sediment inoculum was collected from the bottom and nearshore using a sledge. Plankton was divided into three aerated 100 L tanks: one for sediment and macroinvertebrates, one for large plankton (>140 μm), and one for small plankton (unfiltered water and 20 μm samples).

2.4. Sampling and Analyses

Sampling was carried out weekly and all mesocosms were sampled for the basic physicochemical and biological variables. Physical variables such as temperature, conductivity, salinity, dissolved oxygen, and pH were logged with portable sensors (YSI ProDSS). In addition, dissolved oxygen and temperature were continuously monitored. Water transparency was measured using a Secchi disc. Depth-integrated water column samples for plankton and water chemistry analyses were collected with

a tube sampler. Nutrients such as TN, TP were analyzed by alkaline persulfate oxidation method using a Seal Analytical (Norderstedt, Germany) AA3 autoanalyzer, while NO₃+NO₂ and SRP were measured using the ammonium molybdate–ascorbic acid reduction method (Mackereth et al., 1978). 500 mL of water was taken from each mesocosm and filtered using ISOLAB GF/C (1.2µm pore size) filters for chlorophyll-a analysis. In accordance with protocol described in (Jespersen & Christoffersen, 1987), the samples were refrigerated at +4 °C for 24 hours in 10 mL (*v*) of ethanol. After the samples were centrifuged for 4 minutes at 5000 rpm in the centrifuge machine, the amount of chlorophyll was measured in µg/L in the spectrophotometer at 663 nm (*Abs*₆₆₅) and 750 nm (*Abs*₇₅₀) wavelength. Total chlorophyll- a concentration was calculated using with the formula given below [1].

$$\text{Total chlorophyll} = 11.0([Abs]_{665} - [Abs]_{750}) \times v/Vp. \quad [1].$$

In this formula, *A*₆₆₃ and *A*₇₅₀ are the absorbance readings at 663 and 750 nm wavelength respectively. 11 represents the specific extinction coefficient, while *v* is the amount of solution used to dissolve the chlorophyll in the filter. The filtered volume (*V*) represents the amount of water passing through the filter. *p* refers to the path length that light travels through the sample cuvette in a spectrophotometer (1cm).

For suspended solids analysis, 500 mL of water was collected from the composite water sample and filtered through a dried and pre-weighed GF/C filter. The filters were then dried in an oven at 105 °C for 12 hours. After drying, the filters were weighed again. Total suspended solids (TSS) were calculated using the formula given below [2].

$$\text{Total Suspended Solid (mg/L)} = [(Final\ weight\ of\ filter - Initial\ weight\ of\ filter) \times 1000] / Filtered\ volume\ (mL) \quad [2].$$

2.5. Zooplankton Sampling and Identification

Ten liters of water were collected by the tube sampler from the mesocosms each week by filtering through 45 μm mesh. Filtered zooplankton samples were transferred into 50 mL amber glass bottles and preserved with 4% Lugol's solution to prevent decomposition prior to analysis. Zooplankton were identified to the species level whenever feasible. For identification Thorp & Rogers (2019) and L. A. Bledzki & Rybak (2016) sources were used. An Olympus SZX16 stereo light microscope was used for species identification, and body length measurements were taken using Touptek software. The count was carried out according to the 200/taxon method and samples were counted until 200 individuals of the most abundant species were reached (Mack et al., 2012). Depending on the sample density, 1 mL or 5 mL (in some cases the entire sample) was subsampled using a Pasteur pipette and diluted with distilled water on a counting plate to facilitate identification. Copepods were classified into adults, copepodites, and nauplii, and further divided into calanoids and cyclopoids due to their trophic differences. Biomass, representing the total mass of living matter per unit volume (Wetzel, 2001), was calculated by first measuring the average length of 25 sampled individuals (or the maximum number available), then converting this length to dry weight using literature values, and finally multiplying by their abundance (Dumont et al., 1975; Ejsmont-Karabin, 1998). On 2 November 2023, zooplankton were not observed in mesocosm 1 and mesocosm 9, nor in the sampling events immediately before or after, most likely due to a sampling error; therefore, these data were excluded from the analysis.



Figure 7. Materials and equipment used for zooplankton sampling in the mesocosm experiment

2.6. Data Analysis

All analyses were conducted in R using RStudio. Spearman correlation analysis was used to examine the relationships among physicochemical parameters. Principal Component Analysis (PCA) was used on environmental data to summarize the main environmental trends. Species-level abundance and biomass were used to calculate:

Total zooplankton abundance (ind. L^{-1}),

Total biomass ($\mu\text{g L}^{-1}$),

Community-weighted mean (CWM) body length:

$$CWM = \frac{\sum_i A_i L_i}{\sum_i A_i},$$

where A_i : abundance of species i , and L_i : mean body length.

Species were classified into Rotifera, Cladocera, Coepoda, Ostracoda and other according to taxonomic identity. Linear mixed-effects models were used for total abundance, total biomass, and CWM length due to the presence of replicates and treatments in the experiment. In cases where the model fit was singular (indicating negligible variance in the random effect), the random term was dropped and a standard fixed-effects linear model was applied instead. One-way Analysis of Variance (ANOVA) was used to test for significant differences among groups. Pairwise and Post-hoc analyses were conducted to identify which treatments differed from each other, using Tukey adjusted p-values. Zooplankton community composition was analyzed based on Bray–Curtis dissimilarity. Permutational multivariate analysis of variance (PERMANOVA) was applied to test the effects of salinity and temperature, and non-metric multidimensional scaling (NMDS) was used to summarize multivariate community patterns. Indicator species analysis was performed to identify taxa characteristic of specific treatments or treatment combinations using the `multipatt` function (`IndVal.g` index) in the `indicspecies` R package (Cáceres & Legendre, 2009). The Indicator Value (`IndVal`) was calculated for each species as the product of its specificity (how exclusive the species is to a treatment) and its fidelity (how frequently the species occurs within that treatment) (Dufrêne & Legendre, 1997). This metric identifies taxa that are both restricted to and consistent within specific environmental conditions. Significance was assessed using 9,999 permutations, which were restricted within sampling dates to account for temporal blocking. Prior to analysis, rare taxa occurring in fewer than two samples were excluded. Similarity Percentage (SIMPER) analysis was performed using the `vegan` package in R to identify the specific taxa contributing most to the average dissimilarity between treatment groups (Oksanen et al., 2025). The top 10 contributing taxa for each pairwise comparison were identified (Clarke, 1993). Generalized additive models (GAM) were employed to analyze Shannon diversity and environmental parameters. Relative biomass contributions of major taxa were calculated per sample, and community-weighted mean lengths were calculated in each major taxonomic group. The GAM was simplified by automatically removing

uninformative smooth terms and retaining only those with effective degrees of freedom > 0.5 and $p < 0.20$. The model was checked to ensure reliable predictions using residuals, degrees of freedom, heteroscedasticity, and concurvity.

CHAPTER 3

RESULTS

3. 1. Physico-chemical Response

Temperature profile shown in the figure 8 indicated that mesocosms assigned to warming treatments maintained 4.5 °C higher temperatures than those in no-warming treatments. Towards the end of the experiment, temperatures in the no-warming treatment mesocosms dropped below 15 °C, while those in the warming treatment mesocosms declined to below 20 °C. This decrease was attributable to seasonal decrease in air temperatures in November compared to September.

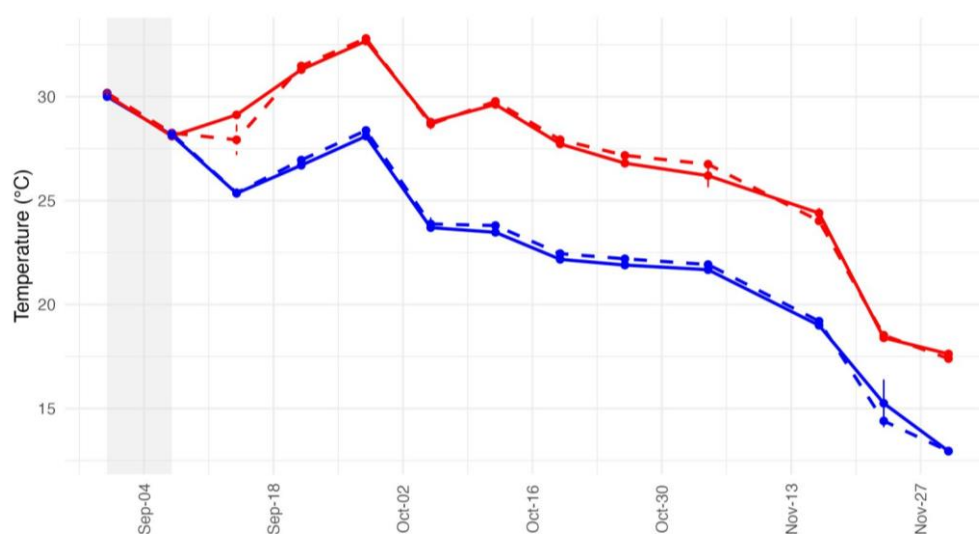


Figure 8. Temperature changes over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.

The experimental design included two salinity levels: 4 g/L and 40 g/L. Between October 2 and October 16, the mean salinity in the 40 g/L warming treatment dropped to approximately 32 g/L due to overflow caused by excess water addition to the some mesocosms. Subsequently, salt was added to adjust the salinity to the intended 40 g/L conditions. Apart from this temporary deviation, salinity levels in all treatments were maintained at their target values throughout the experiment, as shown in Figure 9.

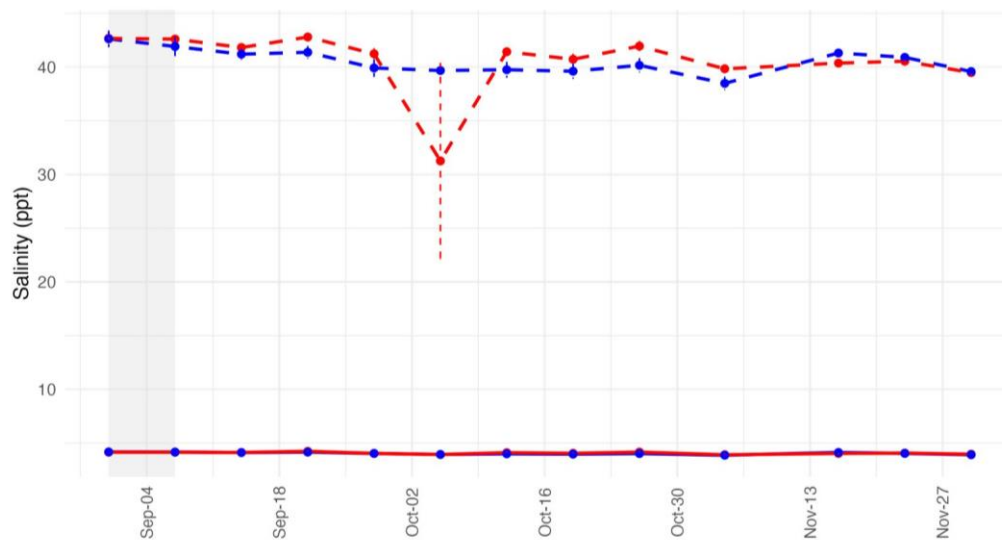


Figure 9 . Salinity changes over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.

In Figure 10, mesocosms with 40 g/L salinity exhibited lower Secchi depth values compared to mesocosms with 4 g/L, indicating higher turbidity. In contrast, mesocosms at 4 g/L showed higher Secchi depths, suggesting lower turbidity and clearer water conditions. Within the 40 g/L treatments, the warming treatment demonstrated higher Secchi depth compared to the 40 g/L non-warming treatment (p-value < 0.05). However, no clear pattern in Secchi depth values was observed between the warming and no-warming treatments at 4 g/L.

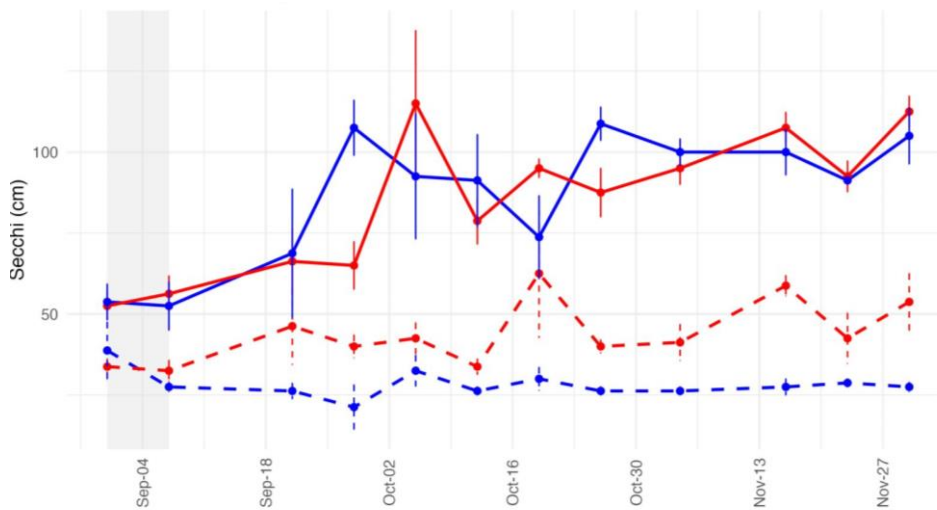


Figure 10. Secchi depth over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.

Chlorophyll-a (Chl-a) concentrations differed significantly across both salinity and temperature treatments ($p < 0.001$ and $p = 0.03$, respectively), except between the 4 g/L no warming and warming conditions. As shown in Figure 11, mesocosms at 4 g/L (regardless of warming) had lower Chl-a levels compared to those at 40 g/L. Initially, chlorophyll-a levels in the 40 g/L no-warming treatment were lower compared to the 40 g/L warming treatment however, in the 40 g/L no-warming treatment, chlorophyll-a levels increased in a fluctuating manner and eventually exceeded those in the 40 g/L warming treatment.

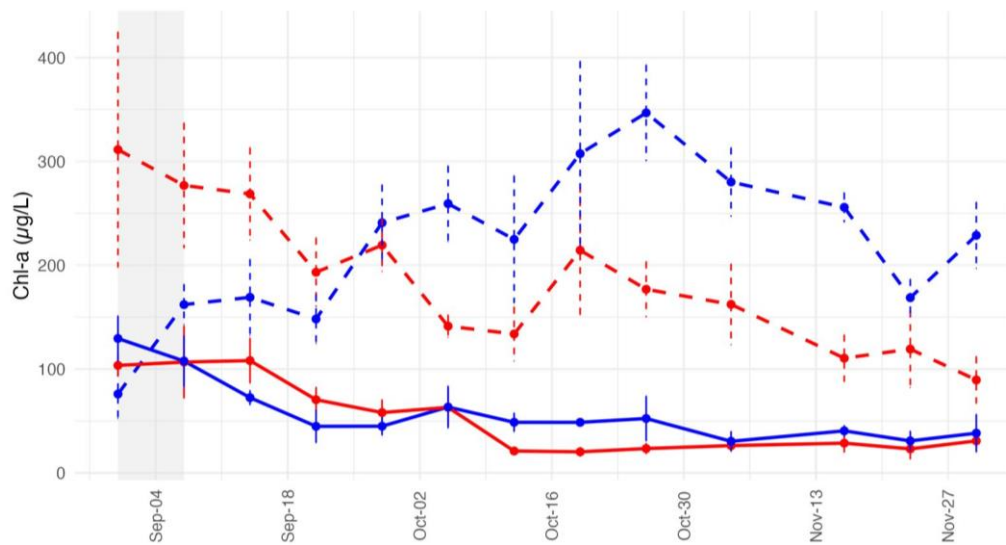


Figure 11. Chlorophyll-a (Chl-a) values over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.

The TSS (total suspended solids) profiles followed a similar pattern as observed for chlorophyll-a showed in figure 12. Mesocosms at 4 g/L consistently exhibited lower TSS concentrations compared to those at 40 g/L, remaining below 100 mg/L throughout the experiment. Among the mesocosms with a salinity of 40 g/L, the no-warming treatment tended to display higher and fluctuating TSS concentrations relative to the warming treatment from the beginning of the experiment. Although ANOVA of the linear model indicated significant difference in TSS values between both salinity and temperature treatments (p-values: 0.0002 and 0.036, respectively), the difference observed only between (40g/L warming - 40g/L no-warming), (4g/L warming - 40g/L no-warming), and (40g/L no-warming - 4g/L no-warming) conditions.

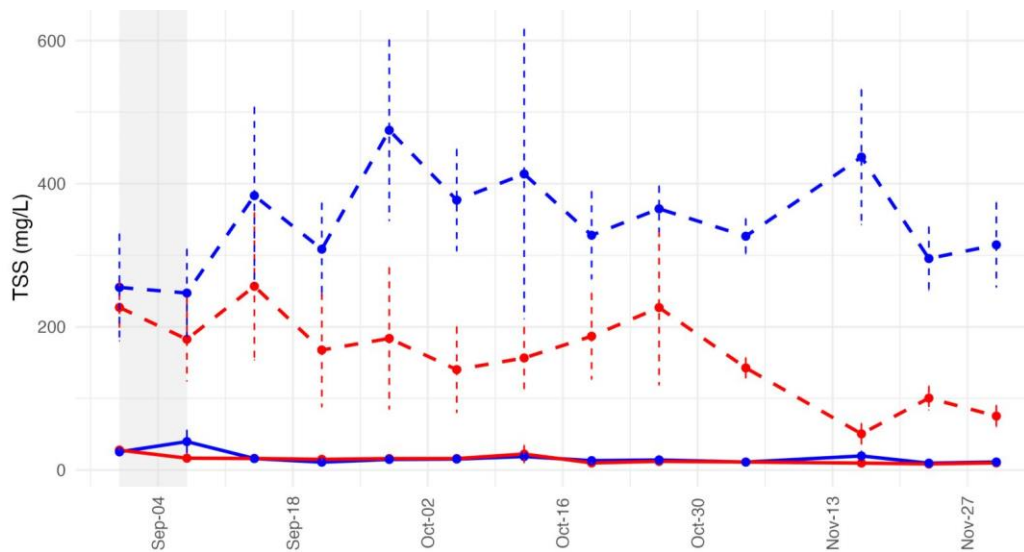


Figure 12. Total Suspended Solid (TSS) values over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.

In Figure 13, DO saturations were significantly higher in no-warming conditions than warming conditions (p -value=0.001). During the pre-heating phase, 4 g/L warming, 40 g/L warming, and 4 g/L non-warming treatments exhibited a decline in dissolved oxygen (DO) concentration. Generally, the 40 g/L warming treatment maintained the lowest percentage of DO compared to the other treatments throughout the experiment. DO values are relatively higher in the 40 g/L no warming treatment compared to the other treatments.

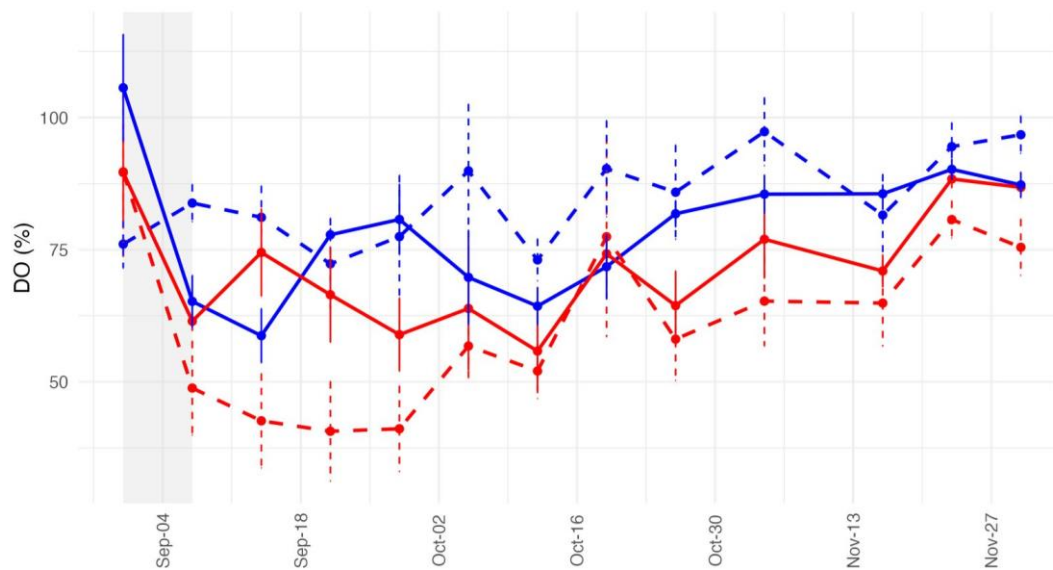


Figure 13 Dissolved oxygen (DO) values over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.

In Figure 14, total phosphorus (TP) levels were lower in the 4 g/L treatments (both no-warming and warming) compared to the 40 g/L treatments (no-warming and warming). Warming treatments generally showed a decrease in TP levels. During the pre-heating phase, TP value in the 40 g/L warming treatment started higher than in the 40 g/L no-warming treatment; however, around September 18 dropped below that of the 40 g/L no-warming treatment and consistently declined throughout the experiment. Overall, the 4 g/L mesocosms had lower TP levels, whereas the 40 g/L mesocosms exhibited higher TP levels.

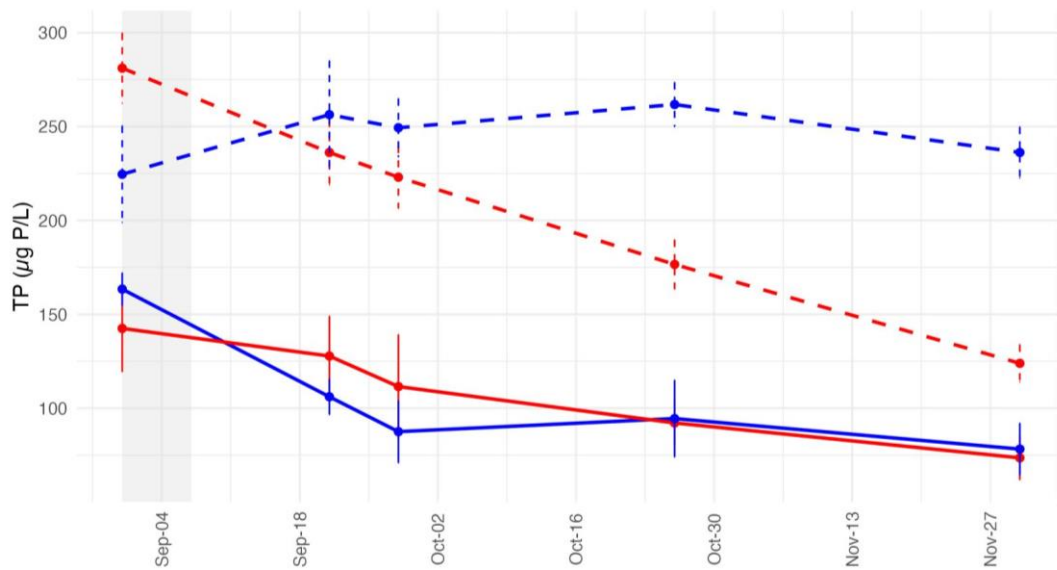


Figure 14 Total phosphate (TP) concentrations over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.

In Figure 15, TN values across all treatments declined from the pre-heating phase until around September 18. The highest TN concentration was observed in the 40 g/L warming treatment (around 4000 $\mu\text{m/L}$), which slightly decreased until about October 30 and then began to increase, following a trend like the 40 g/L no warming treatment. 40 g/L treatments consistently had higher TN levels than the 4 g/L treatments.

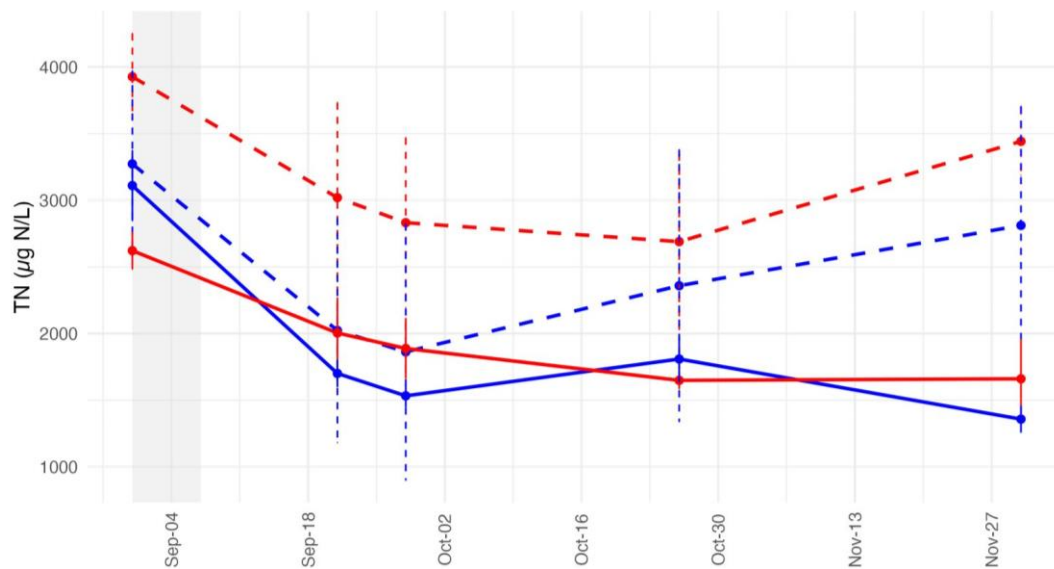


Figure 15. Total nitrogen (TN) concentrations over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.

ANOVA showed no significant overall differences in NO_3^- concentrations between treatments ($p > 0.05$). Both 40 g/L warming and 40 g/L no warming treatments started with around $750 \mu\text{g}$ of NO_3^- and declining to about $170 \mu\text{g}$ in the pre-heating phase. After this phase, the 40 g/L warming treatment had the highest NO_3^- concentrations, reaching approximately $500 \mu\text{g}$ between November 13 and November 27. The 40 g/L no warming and warming treatments exhibited almost the same pattern.

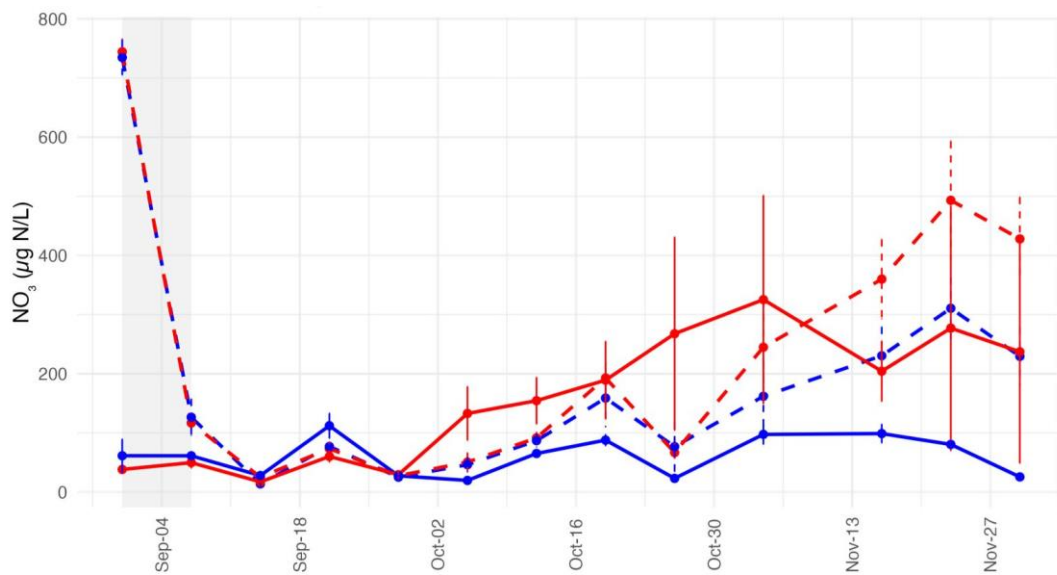


Figure 16 . NO₃ concentrations over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.

In the pre-heating phase, both 40 g/L no-warming and 40 g/L warming treatments showed a decline in SRP and subsequently fluctuated below 20 µg for the rest of the experiment. In contrast, the 4 g/L warming treatment started with a low SRP concentration but generally increased over time, approximately reaching up to 50 µg. Unlike NO₃⁻, SRP concentrations were significantly different between 40 g/L and 4 g/L tanks ($p = 0.018$), where the SRP concentrations in 4 g/L treatments were higher than 40 g/L treatments. However, the Post-hoc test showed that this difference was not significant under no warming conditions (40 g/L no warming vs. 4 g/L no warming, adjusted $p > 0.05$). The significant differences were observed only during the last six weeks, with SRP consistently higher in 4 g/L tanks than in 40 g/L tanks.

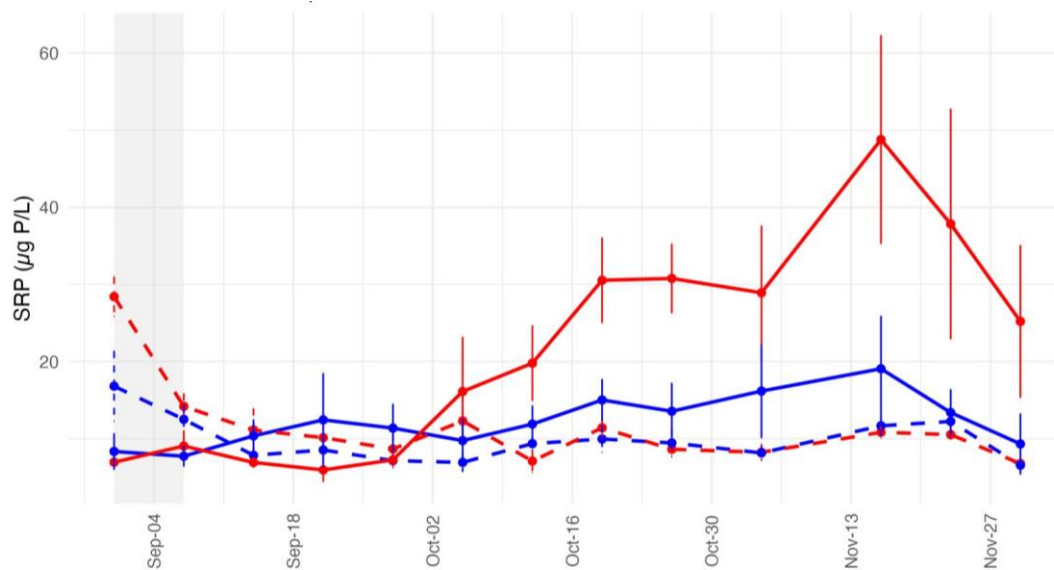


Figure 17. Soluble Reactive Phosphorus (SRP) concentrations over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L). Shaded area represents pre-warming phase.

Figure 18 illustrates the relationships among the physicochemical parameters based on Spearman's correlation analysis. Red stars indicate statistical significance, with significance increasing as the number of stars increases. For example, salinity was strongly and positively correlated with chlorophyll-a and TSS ($R = 0.66$, $p < 0.001$ - $R = 0.72$, $p < 0.001$ respectively) while DO (%) and temperature negatively correlated ($R = -0.62$, $p < 0.001$). Similarly, SRP shows a significant positive relationship with Chl-a, while exhibiting a significant negative relationship with TSS. Salinity shows relationships with all other physical and chemical parameters, despite differences in significant.

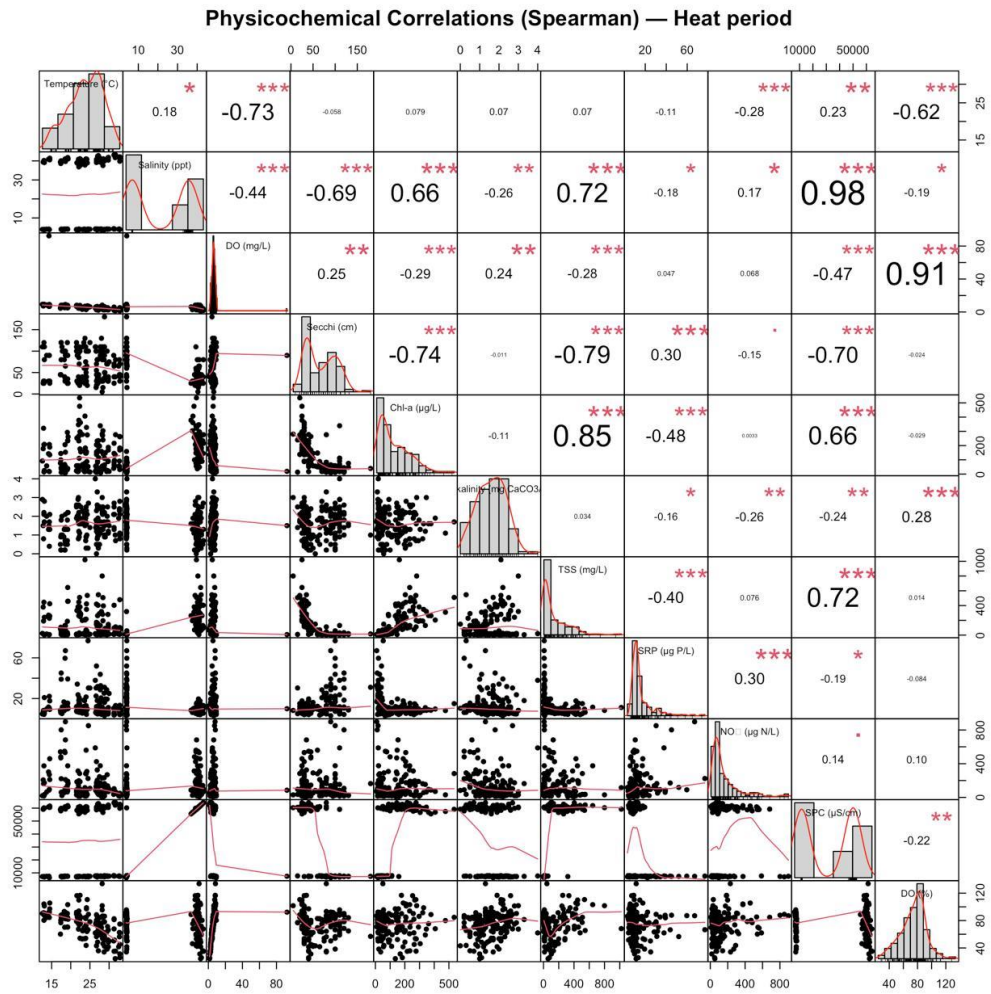


Figure 18. Spearman correlations among physicochemical parameters.

The Figure 19 PCA biplot shows how salinity and other physical factors inter-correlate. The main separation is between high salinity (40 g/L, red) and low salinity (4 g/L, blue). PC1 is mostly correlated with decreasing salinities and increasing Secchi depths. Warming (triangles) and no warming (circles) have smaller effects within each salinity level. Salinity vector points toward the red cluster, indicating an association with high salinity conditions, while Secchi is positioned near the blue cluster, showing a link with low salinity. The statistical analysis showed no significant separation between warming and ambient temperature conditions.

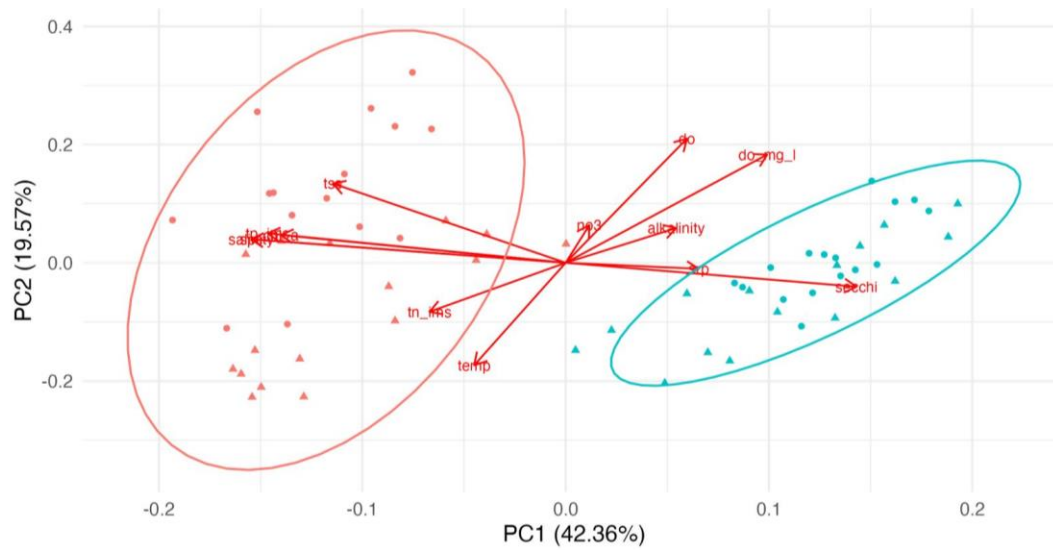


Figure 19. PCA plot of environmental data, triangles for warming, circles for no warming, and colors indicating salinity: blue = 4 g/L, red = 40 g/L.

The PCA biplot shows how samples during the warming period are affected by salinity. PC1 and PC2 explain about 62% of the variation. Low salinity (4 g/L, blue) and high salinity (40 g/L, red) samples formed separate groups. Physicochemical variables point to which conditions are associated with each group: higher secchi depth and DO with 4g/L, temperature, TN, TP, and TSS with 40 g/L. This shows that salinity strongly affects water conditions during the warming period.

3.2 Zooplankton Community Analysis

Table 2. Zooplankton species observed throughout the experiment.

Rotifera	Cladocera	Copepoda
<i>Brachionus plicatilis</i>	<i>Alona costata</i>	<i>Cyclopoid Copepod</i> <i>sp.</i>
<i>Brachionus quadridentatus</i>	<i>Macrothrix hirsuticornis</i>	
<i>Brachionus angularis</i>	<i>Oxyurella tenuicaudis</i>	
<i>Brachionus calyciflorus</i>	<i>Alona sp.</i>	
<i>Lecane ohioensis</i>		
<i>Lecane monostyla</i>		
<i>Lecane luna</i>		
<i>Lecane sp.</i>		
<i>Cephalodella ventripes</i>		
<i>Hexartha</i>		
<i>Euchlanis dilalata</i>		

The Table 2 lists the zooplankton species observed throughout the experiment.

At 40 g/L, the zooplankton community was largely dominated by *Brachionus plicatilis* and *Cephalodella ventripes*, with few additional taxa detected. In contrast, at 4 g/L, a broader range of groups was present, including cladocerans, copepods, and various rotifer species. Empty ostracod carapaces were encountered, which were considered to have possibly resulted from a fixation-related issue. Therefore, they were not included in the analyses.

A linear mixed model (LMM) was first used for total zooplankton abundance, but no random effect was detected (model singular). A linear model (LM) with ANOVA was applied instead. Log-transformed abundance showed strong effects of salinity and warming. Abundance at 40 g/L was higher than at 4 g/L, with the salinity coefficient showing a 2.34-unit increase on the log scale ($p < 0.0001$). Warming also increased abundance ($p = 0.013$). ANOVA indicated both salinity and warming

contributed significantly to total variance, but initial abundance was higher in 40 g/L. The model explained a moderate proportion of the variation (adjusted $R^2 = 0.30$), indicating salinity and warming influenced abundance over time.

Figure 20 shows the contribution of major taxa to total abundance. Rotifers dominated all treatments on 07.09.23 and continued to dominate the 40 g/L treatments on subsequent dates. By contrast, copepods and cladocerans were mainly observed in the 4 g/L treatments on the other three dates. After the first sampling, the abundance of larger zooplankton in the 4 g/L treatments generally increased.

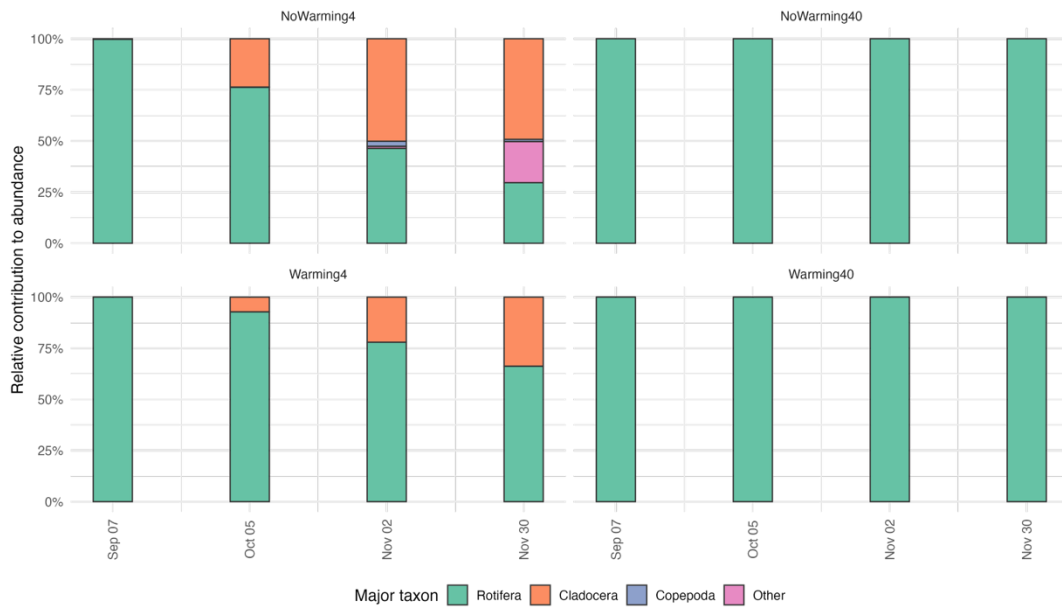


Figure 20. Graph illustrating the relative contributions of major zooplankton taxa to overall community abundance across treatments.

To identify which species contributed most to the differences in abundances observed among treatments, a SIMPER test was performed. The significant differences between the treatments were largely caused by the difference in *Brachionus plicatilis* abundance (average contribution of 30.1%). The other three species that has largest contributions were *Lecane monostyla*, *Lecane ohioensis*, and *Alona costata* with 12.5%, 9.9%, and 8.8%, respectively.

Table 3. Table of species contributing most to abundances according to SIMPER analysis.

Species	Average Contribution (%)
<i>Brachionus plicatilis</i>	26.6
<i>Lecane copeis</i>	13.7
<i>Lecane ohioensis</i>	10.5
<i>Brachionus calyciflorus</i>	10.0
<i>Alona costata</i>	8.3
<i>Hexartha</i>	7.5
<i>Macrothrix hirsuticornis</i>	7.5
<i>Cephalodella ventripes</i>	6.4
<i>Lecane sp.</i>	5.9
<i>Alona sp.</i>	3.6

Figure 21 shows graph of total zooplankton abundance. Zooplankton abundance at 40 g/L was higher than at 4 g/L, mainly due to the high presence of rotifers. At the start of the experiment, abundance was initially high in the 40 g/L treatments; however, the 40 g/L warming treatment showed a decline before beginning to stabilize toward the end of the experiment. In contrast, the 40 g/L no-warming treatment exhibited a clearer and more pronounced decrease. In the second sampling, abundance increased and then started to relatively stabilize again, similar to the pattern observed in the 40 g/L warming treatment. At 4 g/L, zooplankton abundance in the no-warming treatment was slightly lower than that of in the 4 g/L warming treatment.

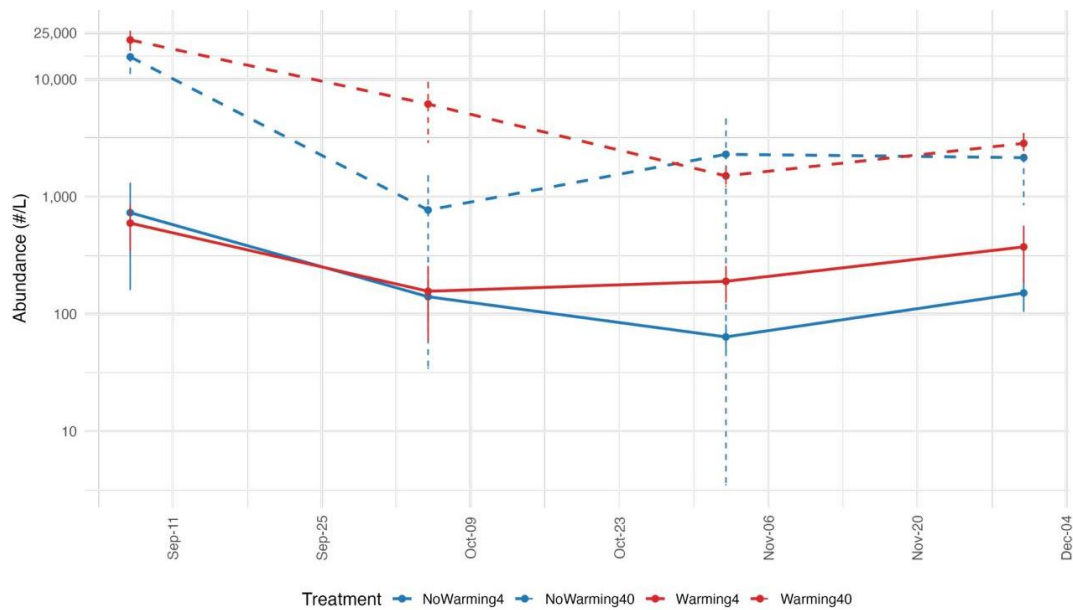


Figure 21. Total zooplankton abundance over time graph. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L) Error bars show standard errors.

The NMDS plot shown below (Figure 22) (stress = 0.124, 2 dimensions) revealed clear separation of zooplankton abundance by salinity treatments (4 g/L vs 40 g/L), consistent with PERMANOVA results. The ellipses represent group variability, with closely positioned points indicating similar communities. The 4 g/L treatments (no-warming and warming) are distributed on the right side of the plot and show greater variability, clustering within the red and blue ellipses. In contrast, the 40 g/L treatments (no-warming and warming) are located on the left side of the plot, with communities closely grouped and enclosed within the green and purple ellipses, indicating higher similarity among these communities.

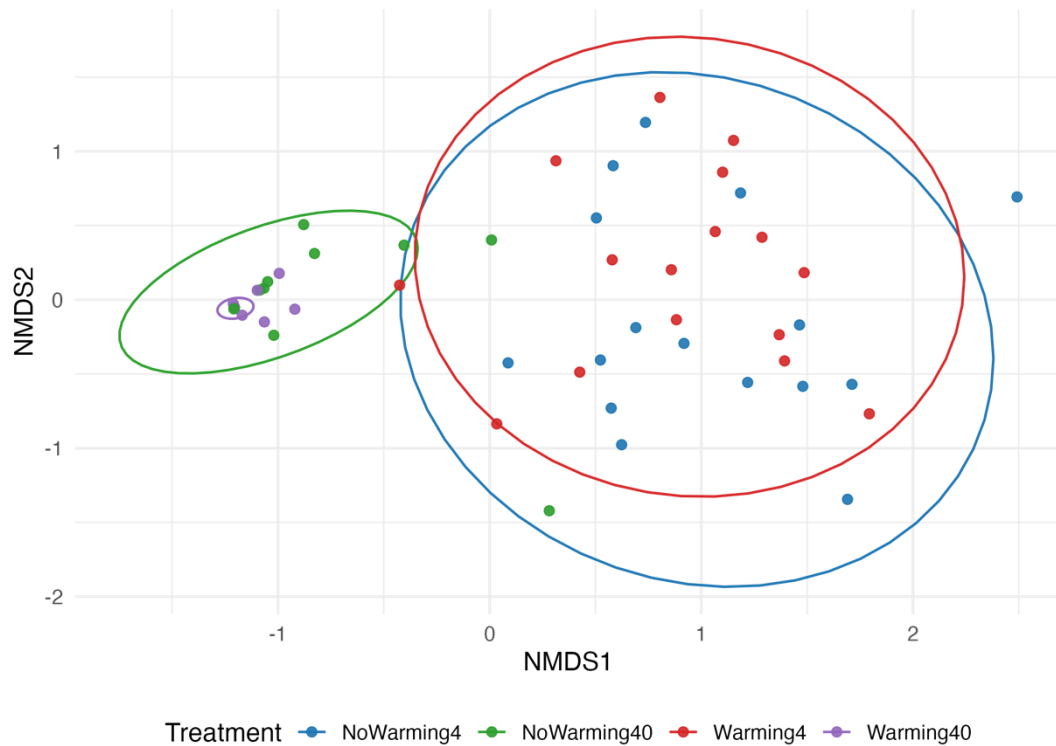


Figure 22. NMDS plot of zooplankton community composition (abundance) based on Bray–Curtis dissimilarities (Stress = 0.124).

Figure 23 shows total biomass composition by major taxon considering all replicates. In the 40 g/L treatments, biomass composition was generally dominated by rotifers. In contrast, in the 4 g/L treatments, biomass was characterized by low rotifer abundance and high cladoceran presence. On the 3rd and 4th sampling dates, in the 4 g/L no warming treatments, copepods, along with rotifers, also contributed to biomass, but to a lesser extent than cladocerans.

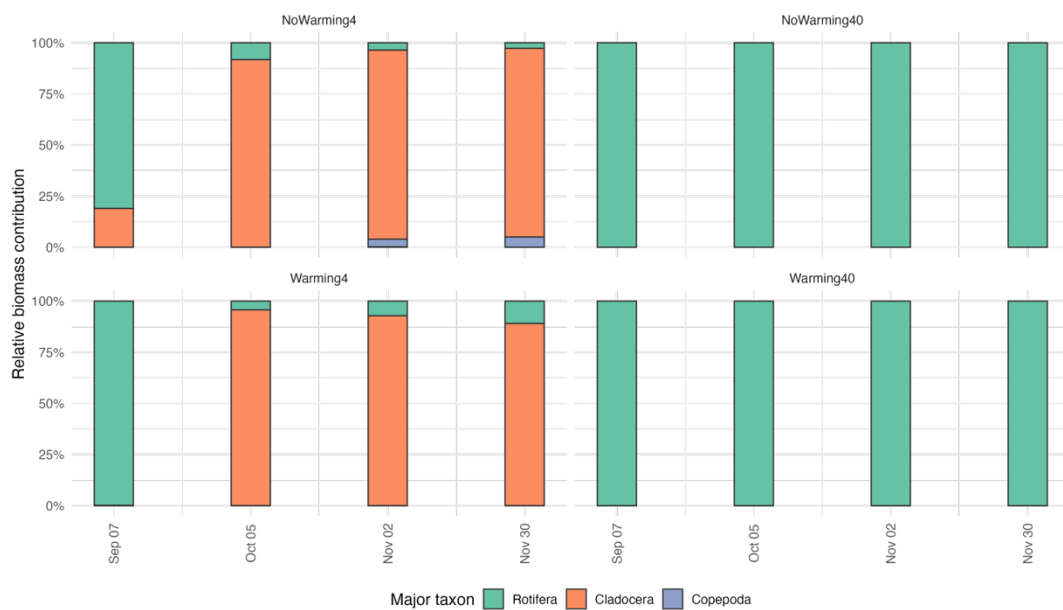


Figure 23. Graph showing total zooplankton biomass composition by major taxonomic groups.

Figure 24 shows the NMDS ordination of zooplankton community structure based on species-specific biomass (stress = 0.098, 2 dimensions). The 4 g/L and 40 g/L treatments are clearly separated, indicating distinct biomass patterns between the two salinity levels, consistent with PERMANOVA results. The ellipses represent group variability, with closely positioned points indicating similar communities. On the right side, the 4 g/L treatments (no-warming in blue and warming in red) show higher variability. On the left side, the 40 g/L treatments (no-warming in green and warming in purple) are more closely grouped, indicating higher similarity among these communities. Overall, the NMDS biomass plot shows a pattern similar to that of the NMDS abundance plot.

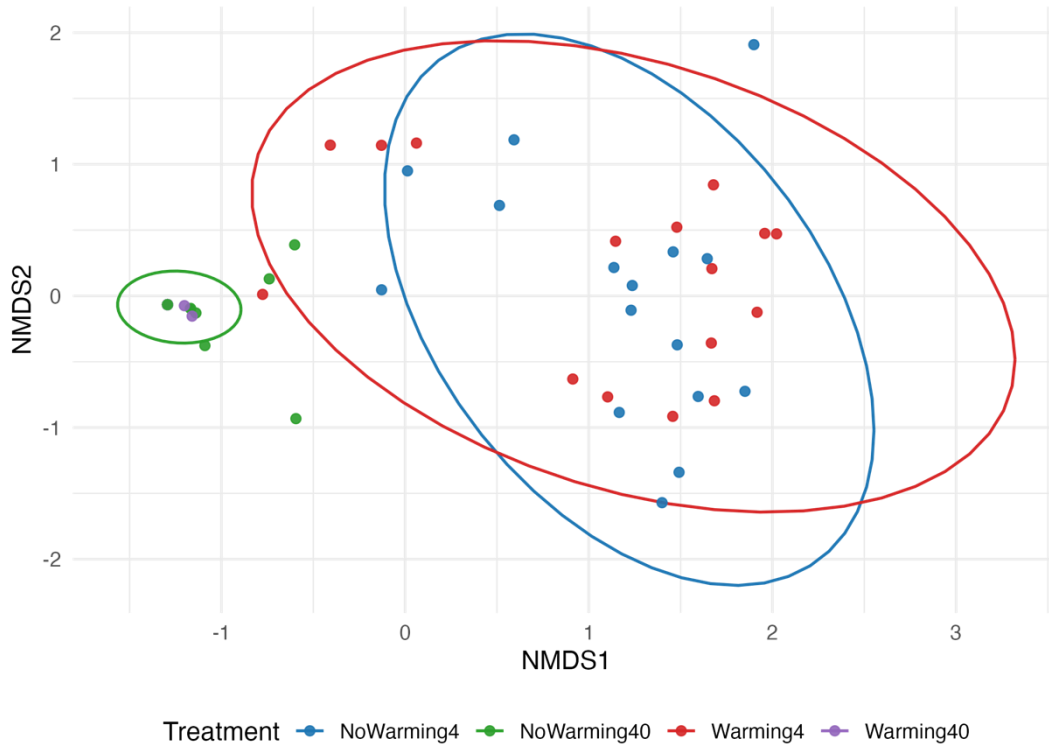


Figure 24. NMDS plot of community structure based on species-specific biomass (stress = 0.098).

Log-transformed biomass showed a modest but significant effect of salinity, while warming had weaker and non-significant effect. Biomass at 40 g/L was higher than at 4 g/L, but the difference was not statistically significant ($p = 0.588$). ANOVA indicated salinity as the main factor ($p = 0.029$). Warming alone did not significantly affect biomass ($p = 0.057$), and the interaction between salinity and warming was not significant ($p = 0.184$).

Biomass composition was used to examine how salinity and temperature affected zooplankton communities. PERMANOVA showed salinity strongly shaped community composition, explaining over half of the variation ($R^2 = 0.52$, $p < 0.001$). Sampling date had a significant effect ($R^2 = 0.09$, $p < 0.001$), and temperature had a smaller but significant effect ($R^2 = 0.01$, $p < 0.001$). Effects of salinity with temperature and salinity with date showed minor changes, while other interactions

were not significant. The model explained 73% of the variation, leaving 27% unexplained. Salinity was the main factor affecting the community.

In Figure 25 the biomass patterns at 4 g/L were nearly identical between treatments, except that the initial biomass in the 4 g/L warming treatment was slightly higher than in the 4 g/L no-warming treatment. Overall, biomass at 4 g/L remained lower than at 40 g/L. In the 40 g/L treatments, initial biomass was higher in the warming treatment compared to the no-warming treatment. By the second sampling date, biomass in the 40 g/L warming treatment had decreased, while biomass in the 40 g/L no-warming treatment increased. Toward the end of the experiment, biomass in both treatments began to converge to similar values.

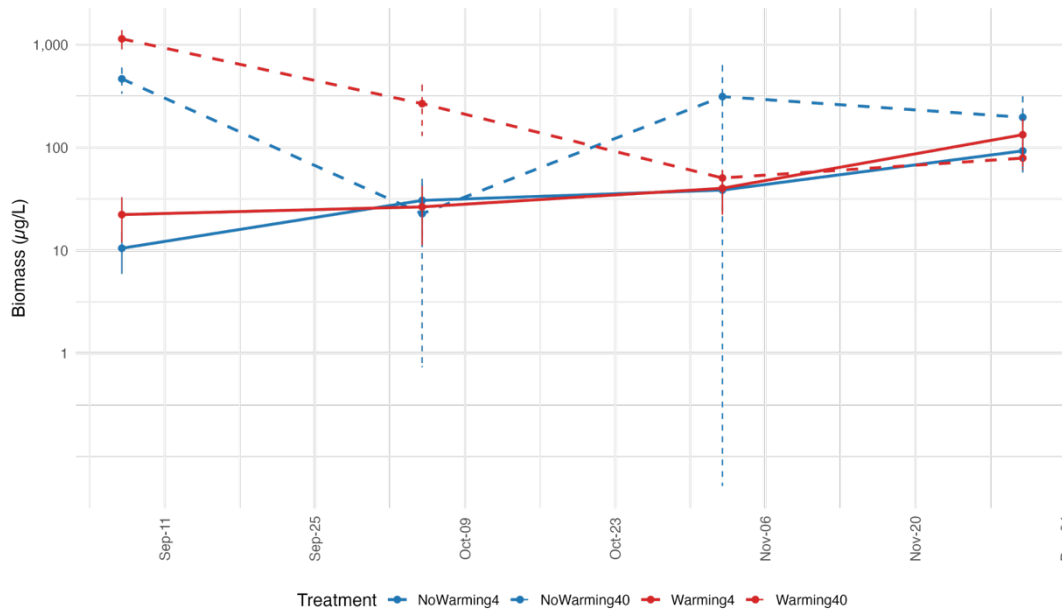


Figure 25. Total zooplankton biomass over time graph. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L).

Figure 26 shows the indicator species for each treatment. In the 40 g/L warming treatment, *Brachionus plicatilis* is the indicator species, whereas in the 40 g/L no-warming treatment, both *Brachionus plicatilis* and *Cephalodella ventripes* are

present as indicator species. At 4 g/L treatments the number of indicator species were more numerous and both 4 g/L treatments, *Lecane copeis* exhibited the highest indicator value (≈ 0.9), followed by *Macrothrix hirsuticornis* and *Alona costata* as the next significant indicator species.

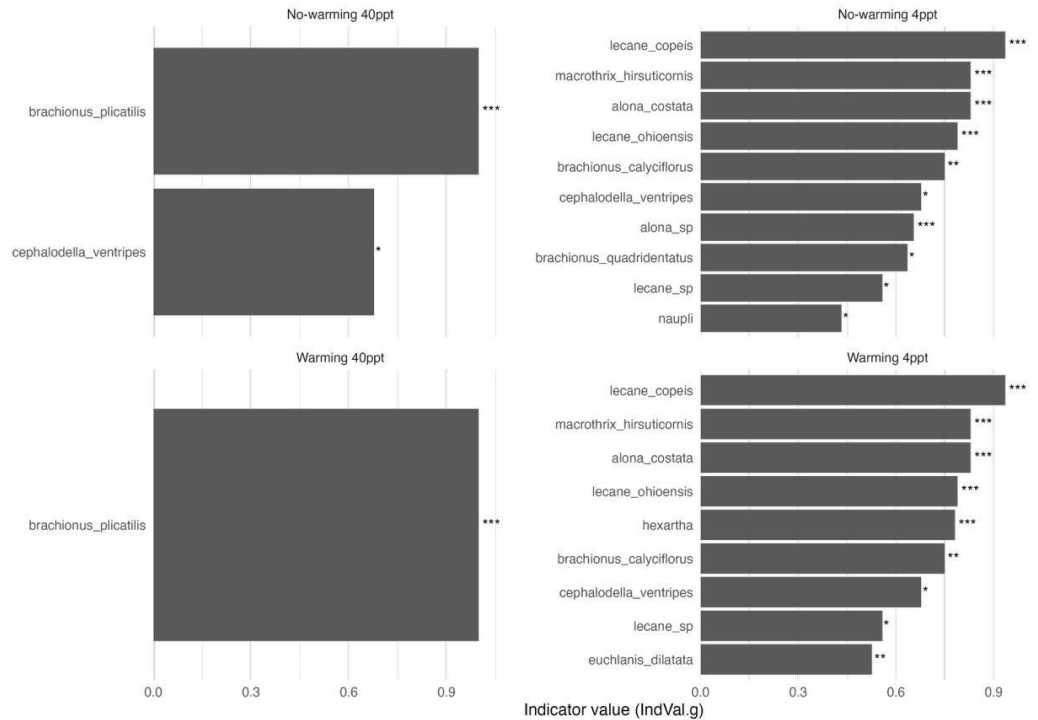


Figure 26. Graph of indicator species per treatment.

Shannon diversity was strongly affected by salinity and to a lesser extent by temperature. Diversity at 40 g/L was lower than at 4 g/L, with the lowest values in the 40 g/L warming treatment (estimate = -0.81 , $p < 0.001$). Warming alone at low salinity did not significantly affect diversity. Secchi depth had a small but significant non-linear effect ($p = 0.023$), while random effects of tank and sampling date were not significant. GAM explained 66% of the variation in diversity (adjusted $R^2 = 0.63$), indicating high salinity, especially with warming, was the main driver of reduced diversity. The Figure 27 shows the model diagnostics of the GAM. The upper left panel shows the estimated smooth effect of the Secchi depth on the

zooplankton Shannon diversity with a 95% confidence interval. The effective degree of freedom was found as 0.86, where the rug plot on the x-axis indicates the distribution. The top-right and bottom-left panels, on the other hand, are the Q-Q plots for the random effects of tank and date, in order to check the normality assumption for the random intercepts.

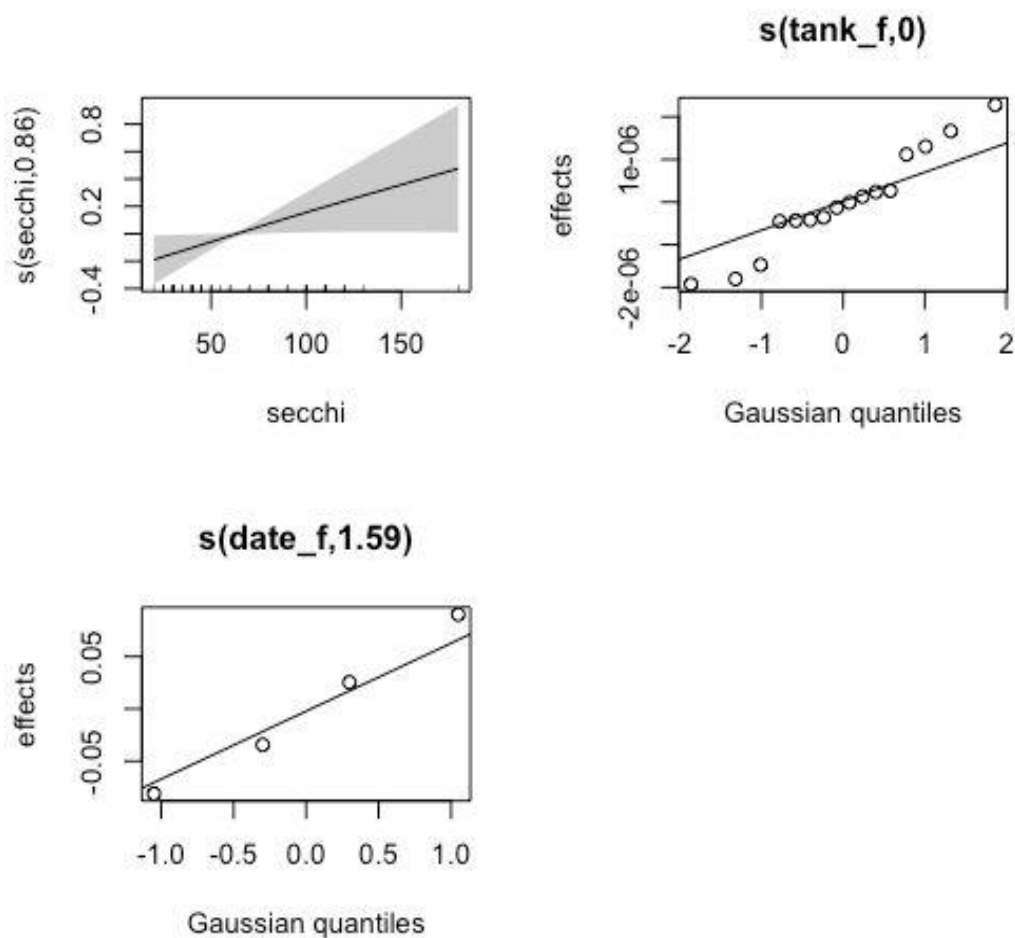


Figure 27. Partial effect plots and model diagnostics from the GAM.

In Figure 28, Shannon diversity is generally higher in the 4 g/L treatments compared to the 40 g/L treatments. In the 4 g/L no-warming treatment, diversity initially declines slightly, then increases considerably before decreasing again. The 4 g/L

warming treatment shows an overall increase in diversity, with a minor decline toward the end of the experiment. In contrast, the 40 g/L warming treatment exhibits the lowest Shannon diversity among all treatments.

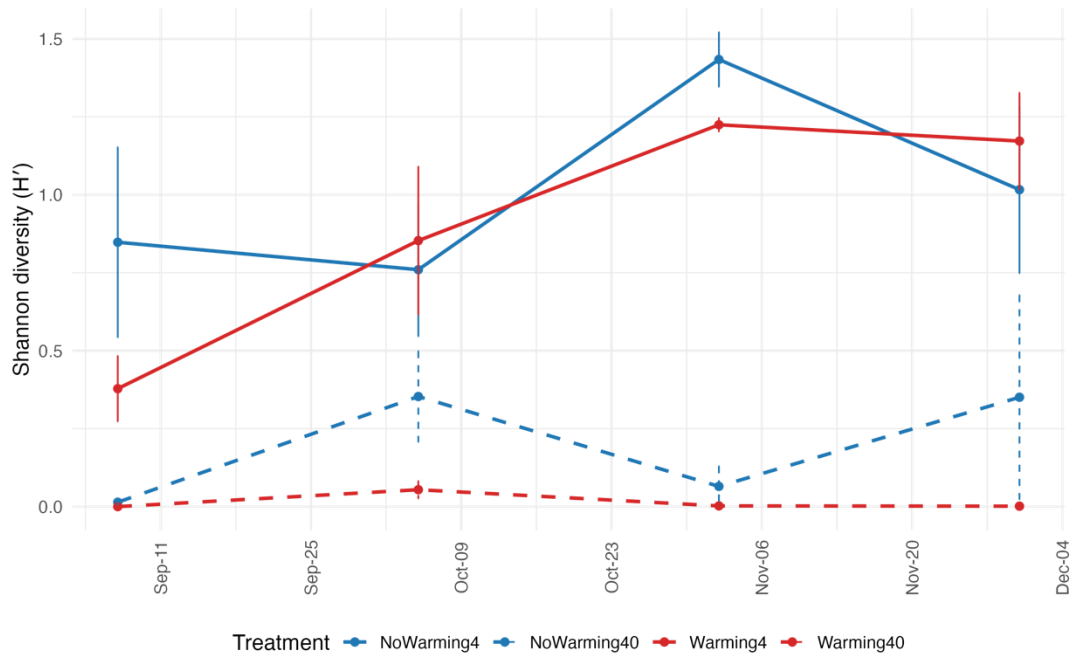


Figure 28. Zooplankton Shannon diversity over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L).

Figure 29 shows zooplankton species richness over time. The lowest richness was observed in the 40 g/L warming treatment, while the highest occurred in the 4 g/L no-warming treatment. The 4 g/L warming treatment exhibited the second highest richness. Overall, species richness patterns inherently mirrored those of Shannon diversity, with 4 g/L treatments generally supporting greater richness than 40 g/L treatments.

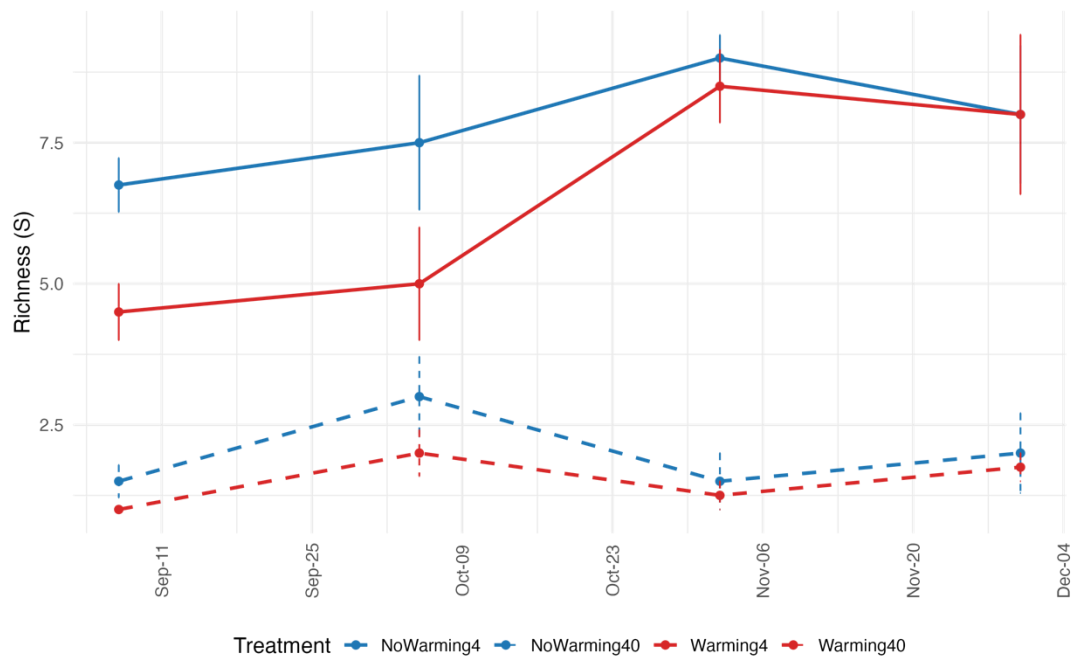


Figure 29. Zooplankton richness over time. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L).

According to the linear mixed-effects model, salinity treatments had a significant effect on community-weighted mean zooplankton body length. In the 4 g/L treatment, the mean body length was 0.19 mm, whereas in the 40 g/L treatment, it was 0.5 mm smaller. This reduction was statistically significant ($p = 0.029$), indicating that high-salinity conditions led to smaller zooplankton body sizes. Variance among mesocosms was negligible, suggesting that the observed changes in body size were not driven by differences between mesocosms. Therefore, increasing salinity caused a significant decrease in zooplankton body size.

For cladocerans, body lengths initially increased in the 4 g/L warming treatment but later declined, while in the no-warming treatments at both salinities, CWM body lengths tended to increase. For rotifers exhibited a decrease in CWM body length under the 40 g/L warming treatment; however, in the 4 g/L warming treatment, rotifer body lengths showed a sharp early decline followed by recovery, and in the 4

g/L no-warming treatment, they increased steadily. At 40 g/L without warming, rotifer CWM body lengths fluctuated throughout the experiment.

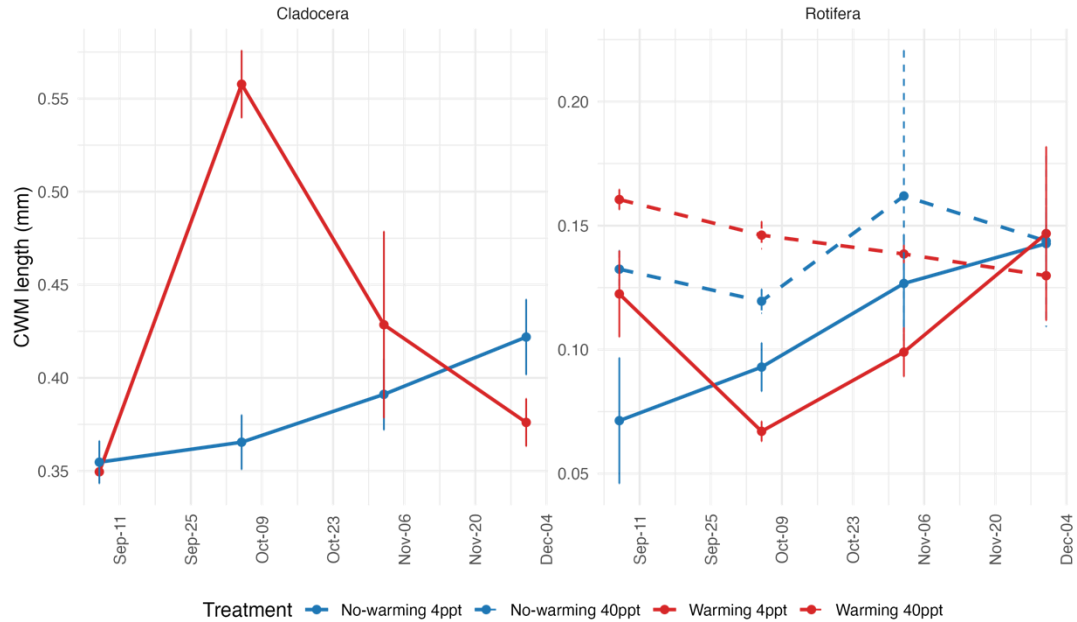


Figure 30. Changes in community-weighted mean (CWM) body length of Cladocera and Rotifera groups. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L).

We examined group-level body sizes, but species can respond differently to salinity and temperature. Average lengths of the relatively most abundant genus were calculated and is shown in Figure 32. Although there were fluctuations in genus average lengths, *Alona* and *Brachionus* genus body length show no significant changes throughout the experiment with the mean sizes approximately 0.35 mm and 0.15 mm, respectively. *Lecane* genus mean body size, on the other hand, seemed to be larger at the end of the experiment despite the fact that statistical analysis revealed no significant variation. In the 4 g/L no-warming treatment, body length of *Brachionus calyciflorus* showed an increase from the beginning. *Brachionus plicatilis* exhibited a decrease in body length under the 40 g/L warming treatment, whereas in the 40 g/L no-warming treatment, body length slightly decreased initially

and then increased. For *Hexarthra*, body lengths in the 4 g/L warming treatment initially decreased but later increased. In the 4 g/L no-warming treatment, body lengths started stable, increased afterward, and then declined. *Lecane ohioensis* in the 4 g/L no-warming treatment first decreased, then increased, and eventually stabilized. In the 4 g/L warming treatment, a slight increase in body length was observed. *Lecane monostyla* initially decreased in both the 4 g/L no-warming and 4 g/L warming treatments, followed by a slight increase; however, towards the end, a decline was observed in the 4 g/L no-warming treatment, whereas an increase was observed in the 4 g/L warming treatment.

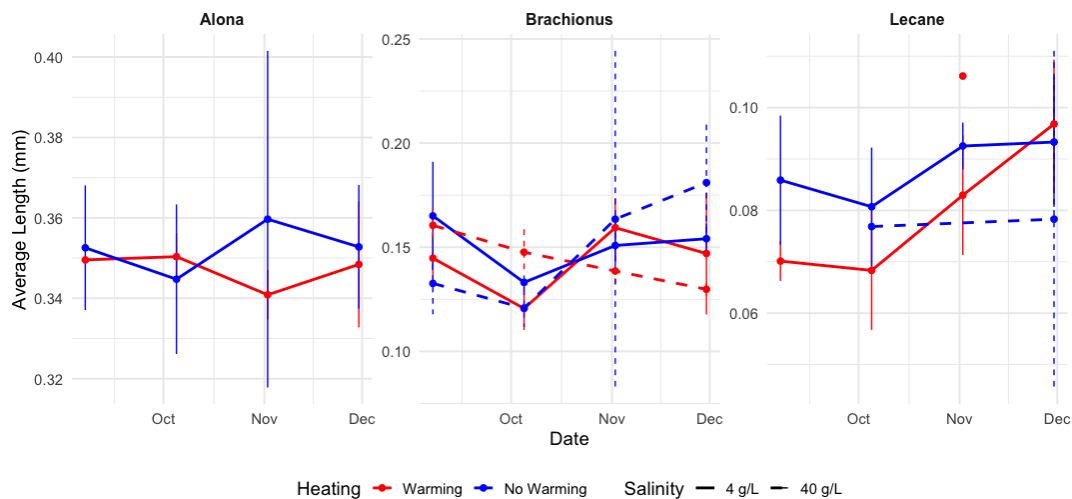


Figure 31. Body length of the most abundant genus. Blue lines: no warming (solid = 4 g/L, dashed = 40 g/L). Red lines: warming (solid = 4 g/L, dashed = 40 g/L).

In Figure 32, the four colors represent the different treatments. The 40 g/L warming and 40 g/L no warming groups cluster on the left side, whereas the blue and purple groups are distributed toward the right. Species composition was strongly influenced by salinity ($R^2 = 0.52$, $p = 0.001$) and dissolved oxygen ($R^2 = 0.33$, $p = 0.004$). The brackish-tolerant species *Brachionus plicatilis* was associated with high salinity, while cladocerans (e.g., *Alona costata*, *Oxyurella tenuicaudis*) and copepods were more strongly related to dissolved oxygen and water transparency (Secchi depth).

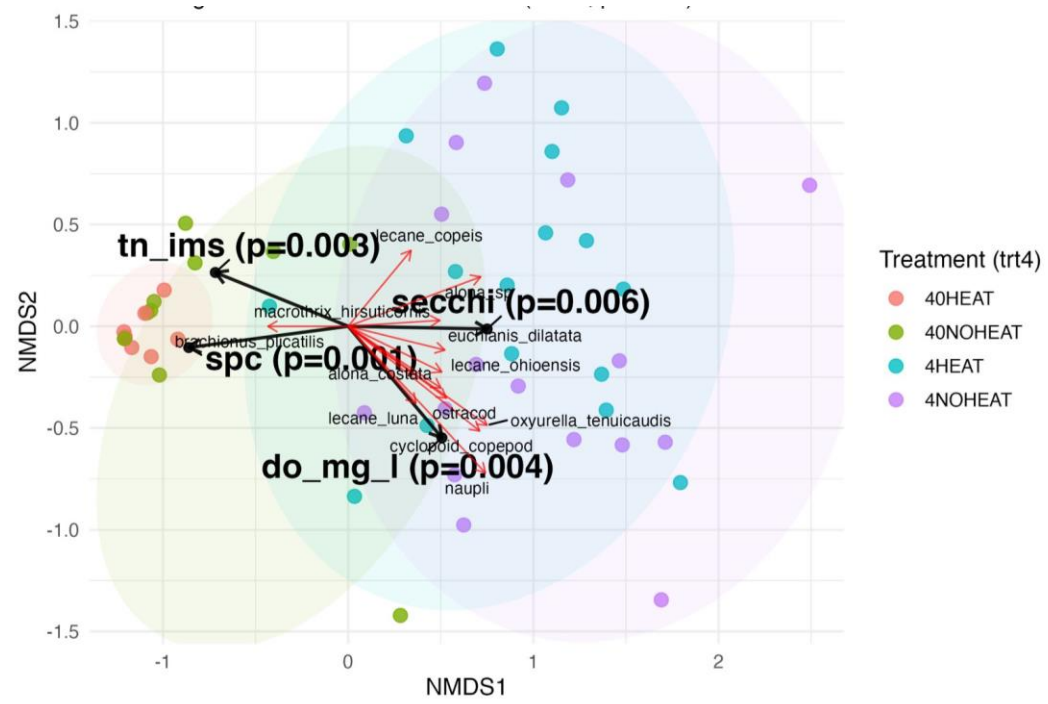


Figure 32. NMDS plot showing the relationship between environmental parameters and species composition.

Table 4 summarizes the PERMANOVA results obtained for the zooplankton community. Salinity emerged as the primary driver of variation, with the 40 g/L treatments consistently exhibiting higher abundance and biomass, whereas the 4 g/L treatments supported larger average body lengths. Warming effects were detected only in specific cases: a significant influence on abundance at high salinity and on average body length. Notably, these effects did not reflect simple shifts in mean values. Instead, the differences were largely attributable to changes in variability among replicates. Warming led to markedly unstable abundance dynamics at high salinity, while acting as an environmental filter on body size, resulting in reduced variance relative to the no-warming treatments.

Table 4. Pairwise PERMANOVA results showing the effects of salinity, temperature, and their combined impact on zooplankton total biomass, average body length, and abundance across treatments. Stars indicate statistically significant

differences, while the position of the arrows (left or right of the significance symbol) denotes which treatment exhibited the higher value. Blue arrows denote directional, mean-driven treatment effects, whereas pink arrows indicate variance-driven effects resulting from increased among-replicate variability rather than consistent shifts in mean values.

Difference	Treatments	Pairwise Permanova Results		
		Abundance	Biomass	Average Length
Only Salinity	NoWarming4 vs NoWarming40	*** ↑	*** ↑	↑ ***
	Warming4 vs Warming40	*** ↑	*** ↑	↑ ***
Only Warming	NoWarming40 vs Warming40	*** ↑	-	↑ ***
	NoWarming4 vs Warming4	-	-	↑ *
Warming + Salinization	Warming4 vs NoWarming40	*** ↑	*** ↑	↑ ***
	NoWarming4 vs Warming40	*** ↑	*** ↑	↑ ***

p-value; - : >0.5; *:<0.05; ***: <0.01

CHAPTER 4

DISCUSSION

Salinity and warming treatments induced significant changes in water clarity, reflecting their influence on the physical characteristics of the water column. Secchi depth was higher in the 4 g/L mesocosms and lower in the 40 g/L mesocosms. At the same time, both chlorophyll-a and TSS values were higher at 40 g/L. The reduced Secchi depth under high salinity conditions can be attributed to increased concentrations of suspended solids, which limit light penetration, and elevated chlorophyll-a levels, which serve as a proxy for phytoplankton biomass and contribute to water column turbidity (Harvey et al., 2019).

The lowest dissolved oxygen (DO) values were observed in the 40 g/L warming treatment. This pattern can be explained by well-established physical and chemical principles: as water temperature increases, the solubility of oxygen decreases, meaning that warmer water naturally holds less dissolved oxygen (Yavuz, 2025). Additionally, higher salinity further reduces oxygen solubility due to the presence of dissolved ions, which effectively displace oxygen molecules in the water (Sherwood et al., 1991). Therefore, the combination of elevated temperature and high salinity in the 40 g/L warming mesocosms is consistent with the observed low DO levels. This trend is further supported by the Spearman correlation analysis, which shows that both temperature and salinity are negatively and significantly correlated with DO ($\rho = -0.73$ and -0.44 , respectively). Consistent with this pattern, in the 4 g/L salinity treatments, DO concentrations were lower in the warming treatment compared to the no warming treatment, further confirming the negative effect of elevated temperature on oxygen availability. Higher DO is expected in 4 g/L no-warming conditions. However, biological activity also influences oxygen levels. In our study, the highest DO was observed in the 40 g/L no-warming mesocosms. Although high ion

concentrations in this treatment would normally reduce oxygen solubility (Benson & Krause Jr., 1984), the low temperature and increased biological activity appear to have outweighed this effect, resulting in higher DO.

In the 40 g/L salinity mesocosms, higher TSS values were observed, likely due to multiple factors. Elevated chlorophyll-a levels indicate greater primary production, leading to the accumulation of organic particles such as dead phytoplankton and plant detritus in the water column. Additionally, dissolved ions in the saline water may have influenced particle suspension, further contributing to increased TSS (Li et al., 2025). Between the 40 g/L mesocosms, TSS concentrations were higher in the no-warming treatment than in the warming treatment, likely because warming enhanced particle flocculation and subsequent settling (Qiao et al., 2019). Spearman correlation analysis supports these observations: TSS was positively and significantly correlated with chlorophyll-a ($\rho = 0.85$) and salinity ($\rho = 0.72$) and negatively correlated with Secchi depth ($\rho = -0.79$). These results suggest that higher primary production and salinity contribute to increased suspended solids, which in turn reduce water clarity. The pattern observed in TSS was also reflected in chlorophyll-a values, which were higher in the 40 g/L treatments and low in 4 g/L treatments. In the 40 g/L warming treatment, chlorophyll-a generally decreased over time, whereas in the 40 g/L no-warming treatment, it showed a relative increase. As mentioned above, chlorophyll-a serves as a proxy for primary production. While warming can enhance metabolic activity, the combined effects of high salinity and elevated temperature may have had an inhibitory effect on overall phytoplankton growth (Chakraborty et al., 2021). Under high salinity conditions, many species experience stress, but salinity tolerant taxa such as certain cyanobacteria may have proliferated, contributing to the observed increase in chlorophyll-a in the 40 g/L treatments (Pade & Hagemann, 2014). Consequently, the decomposition of this abundant biomass in the water column likely released additional nutrients, contributing to the observed increase in TP and TN in these treatments.

The low SRP concentrations in both 40 g/L treatments (warming and no warming) may result from uptake by abundant primary producers, a phenomenon consistent with standard nutrient drawdown dynamics in phytoplankton-dominated systems (Reynolds, 2006; Sommer et al., 2012). In contrast, in the 4 g/L warming treatment, chlorophyll-a concentrations were among the lowest in more than half of the experiment, particularly after October 2, indicating a low abundance of primary producers and, consequently, fewer organisms to uptake SRP, which explains the elevated SRP concentrations. Also elevated SRP values observed under the 4g/L warming treatment may be attributed to enhanced microbial activity in the sediments induced by higher temperatures (Zhou et al., 2016).

NO₃ concentrations, like TN, were initially high in the 40 g/L treatments (both warming and no warming) but exhibited a rapid decline likely due to enhanced uptake by abundant primary producers. This pattern of rapid nitrate depletion during periods of high algal biomass is a well-documented feature of phytoplankton nutrient assimilation (Reynolds, 2006; Wetzel, 2001). In the warming 4 g/L treatment, chlorophyll-a concentrations were among the lowest in more than half of the experiment, indicating lower primary producer existence; consequently, TN and NO₃ levels remained relatively high across 4 g/L mesocosms. Similarly, SRP concentrations were also elevated in this treatment, consistent with the low chlorophyll-a concentrations allowing dissolved nutrients, including nitrogen and phosphorus, to accumulate in the water column.

PERMANOVA results further indicated that salinity was the dominant factor in this experiment, which included both temperature and salinity treatments. High salinity likely decreased dissolved oxygen through the salting-out effect of dissolved ions, while simultaneously promoting higher TSS and chlorophyll-a concentrations via the proliferation of salinity-tolerant species (Al-Tae, 2018).

Salinity and warming treatments further elicited significant responses in zooplankton communities. In the indicator species analysis *Brachionus plicatilis* was identified among the indicator species in the 40 g/L treatments, a finding aligned with its well-

documented tolerance to hypersaline conditions (Snell, 1986). In addition to *B. plicatilis*, *Cephalodella ventripes* was observed in the 40 g/L no-warming treatment; however, it was not identified as an indicator species in the warming treatment, suggesting that it might have been tolerant to high salinity but less prominent under the combined stress of high salinity and elevated temperature or their numbers were low. Species can exhibit different responses to environmental factors. In the 4 g/L treatments, the three indicator species were *Lecane monostyla*, *Macrothrix hirsuticornis*, and *Alona costata*, consistent with the preference of the latter two cladocerans for oligohaline waters (Boronat et al., 2001). Additionally, *Hexarthra sp.* and *Euchlanis dilatata* were identified as indicator species in the 4 g/L warming treatment, whereas they were not present as indicators in the 4 g/L no-warming treatment, highlighting the context-dependent nature of species performance under different environmental conditions (Fernández et al., 2022). This specific emergence of *Hexarthra sp.* under warming is consistent with ecological niche analyses which classify this genus as a characteristic summer taxon, occupying a distinct warm-water niche separated from spring and winter species (Miracle, 1974). Thus, its dominance in the warming treatment likely reflects a competitive advantage triggered by the warming conditions.

When considering the direct effects of salinity, increased salinity levels impose physiological stress on zooplankton by disrupting their osmoregulation processes (Sun et al., 2023). This directly influences survival, growth, and reproduction. High salinity leads to the decline of low-tolerance species and allows only halotolerant taxa to persist; in our case, rotifers became the dominant group under 40 g/L conditions. Increased salinity particularly stresses larger zooplankton species, giving a competitive advantage to small-bodied, salt-tolerant rotifers (Ersoy et al., 2022).

Moreover, in our experiment, warming did not have a detectable effect on zooplankton body size. However, it is expected that under a sufficiently strong warming treatment in future experiments, zooplankton could exhibit a reduction in body size. Zooplankton typically respond to elevated temperatures by decreasing

their body size due to increased metabolic demands and accelerated developmental rates, which shorten growth periods (Albini et al., 2025; Yvon-Durocher et al., 2011). A temperature-driven reduction in body size may also diminish the amount of energy transferred to higher trophic levels in the food web, potentially weakening overall food-web structure and stability (Fernando, 1994).

Although phytoplankton composition was not examined in this study, salinity affects not only zooplankton but also phytoplankton groups, thereby shaping the quality and quantity of food available to zooplankton (Karakuş et al., 2022; Ligorini et al., 2023). In addition, in denser (saltier) water, larger zooplankton may need to expend more energy for swimming and foraging, which can further contribute to their reduced performance under high-salinity conditions (Zadereev et al., 2022).

Zooplankton biomass was lower in the 4 g/L treatment than in the 40 g/L treatment, where the salinity-tolerant rotifer *Brachionus plicatilis* flourished in the absence of fish. Although we did not directly measure the effects of fish predation or macrophyte refuge, literature suggests that fish can exert top-down control on zooplankton, while macrophytes may provide refuge and partially buffer against predation (Kluijver et al., 2015; Vanni, 1986). These factors likely contributed to the observed differences in biomass between treatments.

The absence of macrophytes in the 40 g/L treatment might have promoted phytoplankton growth by removing both nutrient competition and shading effects (Hilt & Lombardo, 2010; Mulderij et al., 2007). Without macrophyte shading, more light may have supported higher phytoplankton biomass. These combined bottom-up (salinity-driven phytoplankton changes) and top-down (fish predation) mechanisms highlight that the observed zooplankton patterns might have arisen from multiple interacting stressors rather than from salinity alone.

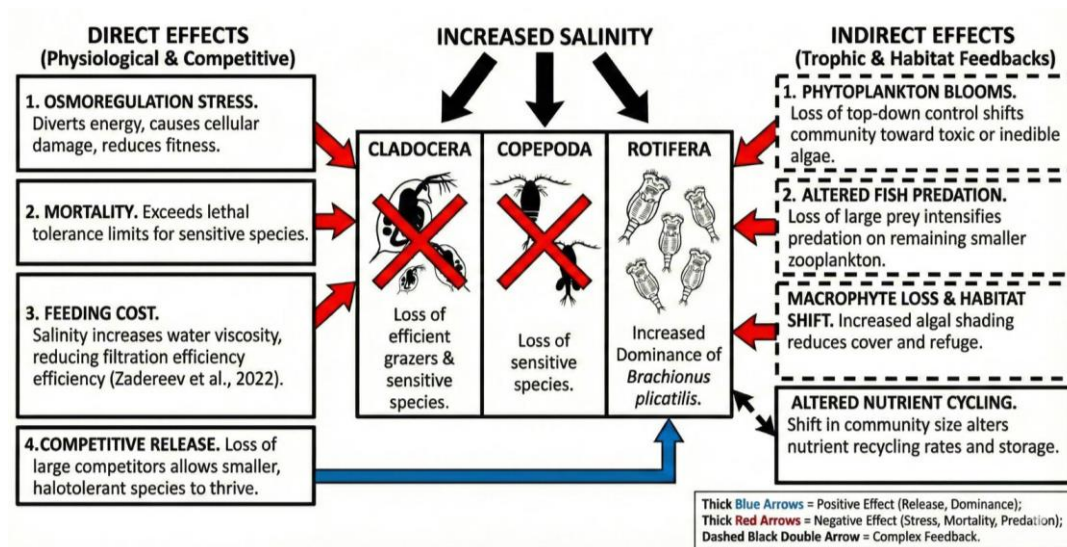


Figure 33. Representation of the direct and indirect impacts of salinity on zooplankton communities.

In our initial hypothesis, we expected that in the 40 g/L treatments, large zooplankton groups would be replaced by less efficient rotifer communities, whereas in the 4 g/L treatments, larger zooplankton groups would remain more abundant. In the experiment, only rotifers were observed in the 40 g/L treatments, while the 4 g/L treatments hosted a more diverse community with larger zooplankton groups. Overall, a clear community shift occurred between the 4 g/L and 40 g/L treatments.

Zooplankton abundance was lower in the 4 g/L mesocosms compared to the 40 g/L treatments. This pattern can be attributed to the presence of larger-bodied taxa, such as cladocerans, alongside rotifers in the 4 g/L tanks. Larger-bodied zooplankton generally exhibit slower reproductive rates and longer generation times compared to smaller-bodied taxa, which limits their contribution to total abundance despite their biomass (Jiang et al., 2017). In contrast, the 40 g/L treatments were largely dominated by the salinity-tolerant rotifer *Brachionus plicatilis*, whereas larger-bodied taxa were largely absent, likely due to their limited capacity for osmotic regulation under high salinity conditions (Zsuga et al., 2021). Consequently, smaller rotifers, with shorter generation times and higher reproductive output, reproduced

more rapidly and contributed disproportionately to overall abundance. Supporting this, SIMPER analysis indicated that *Brachionus plicatilis* accounted for 26.6 % of the total community contribution.

Total abundance, as well as total biomass, showed a declining trend over time. This pattern likely reflects the natural life cycle and density-dependent stress of the dominant species, *Brachionus plicatilis* (K. F. Walker, 1981). Although initial populations were high, natural mortality, intraspecific competition, and seasonal community senescence in autumn likely contributed to the observed decreases in both abundance and biomass (DeMott, 1989; Steiner, 2003).

In terms of total biomass composition, the 40 g/L treatments were predominantly composed of the salinity-tolerant rotifer *Brachionus plicatilis*, whereas in the 4 g/L treatments, biomass was distributed among rotifers and larger-bodied zooplankton. Although larger zooplankton such as cladocerans contributed disproportionately to biomass due to their greater body size, their low abundance meant that total biomass in the 4 g/L treatments remained lower than in the 40 g/L tanks. In contrast, the high numerical abundance of small rotifers in the 40 g/L treatments drove higher overall biomass, which decreased slightly over the course of the experiment.

Zooplankton diversity, measured as both species richness and Shannon diversity, was higher in the 4 g/L treatments than in the 40 g/L treatments. Lower salinity likely allowed a broader range of species to persist, whereas the harsher conditions at 40 g/L favored only a few stress-tolerant taxa, particularly the rotifer *Brachionus plicatilis*, leading to reduced richness and dominance-driven declines in Shannon diversity. Within the 4 g/L treatments, richness and diversity were lower under warming, suggesting that elevated temperature combined with salinity stress reduced community resilience. The 40 g/L warming treatment had the lowest diversity overall, indicating that combined high salinity and temperature strongly constrained species survival and evenness. These patterns are consistent with global analyses showing that freshwater biodiversity declines sharply beyond specific salinity thresholds (Wang et al., 2025) and with studies demonstrating that salinity and

warming can disrupt zooplankton physiology, reproduction, and growth, thereby reducing both richness and evenness (Echaniz et al., 2012; Paturej & Gutkowska, 2015; von Weissenberg et al., 2022).

Our second hypothesis predicted that species richness, biomass, diversity, and abundance would be lower in the 40 g/L treatments compared to the 4 g/L treatments. The results confirmed that species richness and diversity were lower at 40 g/L; however, this was not the case for biomass and abundance. The high abundance and biomass observed in the 40 g/L treatments were largely driven by the salinity-tolerant, small-bodied rotifer *Brachionus plicatilis*. Despite their small size, the high numerical abundance of these rotifers resulted in relatively high total biomass. These findings are consistent with observations from Mediterranean coastal ponds (Anton-Pardo & Armengol, 2012), where increased salinity also caused a decline in zooplankton richness and diversity. In both cases, salinity-tolerant rotifers became dominant, while larger and more sensitive taxa, such as cladocerans, declined or disappeared. This shift indicates that high salinity favors small, resilient rotifers at the expense of larger taxa, reducing community complexity and potentially altering ecosystem processes. Similarly, in a study conducted across 24 lakes in a semi-arid region of northwest China, covering a wide salinity gradient, zooplankton species richness, diversity, and functional diversity were observed to decrease with increasing salinity (Gutierrez et al., 2018).

In a mesocosm study, Ersoy et al., (2022) observed that high chloride concentrations (2.3 g/L) reduced crustacean abundance, taxon richness, and diversity. Consistent with these findings; species richness, diversity and crustacean abundance were lower in high salinity (40 g/L) mesocosms compared to low salinity (4 g/L) mesocosms in our study. These results are further supported by a large-scale European study (Hébert et al., 2023), which reported consistent decreases in abundance, taxon richness, and Shannon diversity with increasing chloride concentrations, along with widespread sensitivity across major taxonomic groups, including Cladocera,

Cyclopoida, and Calanoida. Together, these studies provide strong evidence that elevated salinity reduces community diversity, supporting our first hypothesis.

In addition to salinity effects, short-term heat stress is known to reduce zooplankton biomass, particularly among sensitive cladocerans, often through complex interactions with salinity (Sun & Arnott, 2022). However, in contrast to the significant declines reported by Sun & Arnott, (2022), we did not observe a significant main effect of warming. This discrepancy likely stems from the nature of the thermal stress applied. Sun and Arnott simulated acute heatwaves, pulsed stressors involving high thermal variation, whereas our study applied continuous warming. Theoretical and empirical evidence suggests that increased temperature variation often poses a greater risk to population persistence than elevated average temperatures alone (Vasseur et al., 2014). Consequently, the stable warming regime in our experiment may have allowed for physiological maintenance or acclimation (Geerts et al., 2015) preventing the biomass losses typically driven by acute thermal fluctuations.

For our last hypothesis, we predicted that zooplankton body size would decrease under warming treatments, based on the temperature–size rule and previous literature (Atkinson, 1994). For instance, Albin et al., 2025 conducted a large-scale freshwater mesocosm experiment and found a nonlinear decrease in overall mean body size with warming, with a 57% reduction observed at +8 °C. In contrast, our experiment did not reveal a consistent effect of warming on zooplankton body size, suggesting that responses may vary depending on community composition, experimental conditions, or the magnitude and duration of warming (Carter et al., 2017). Specifically, for cladocerans, community-weighted mean (CWM) body length in the 4 g/L warming treatment initially increased and continued to grow until around October 9, after which a decline was observed. In contrast, cladoceran body size increased consistently in both 4 g/L and 40 g/L no-warming treatments throughout the experiment. For rotifer groups, individuals in the 4 g/L warming treatment exhibited a sharp reduction in CWM body length at the beginning of the

experiment, but body length increased after October 9. In the 40 g/L warming treatment, CWM rotifer body length showed only a minor decrease. This observed pattern may reflect short-term adaptive responses of zooplankton or species-specific responses to warming and salinity conditions (Dam, 2013; Pantel et al., 2015). Such variability highlights that body size changes are not uniform across taxa and can be influenced by multiple interacting environmental factors. The observed decrease in body length of *Brachionus plicatilis* under the 40 g/L warming treatment may reflect a physiological response to the combined stress of high salinity and elevated temperature. In contrast, in the 4 g/L warming treatment, the lower salinity likely reduced physiological pressure, resulting in no clear pattern in body length. However, this pattern was observed only in *Brachionus plicatilis*. Prolonged warming or higher temperatures could make this pattern more pronounced.

Overall, these results indicate that the expected warming-induced reduction in zooplankton body size was not consistently observed, and therefore our hypothesis regarding size-mediated impacts was not supported.

The presence of fish in the 4 g/L mesocosms might have influenced zooplankton abundance and, indirectly, total biomass through predation pressure, although macrophytes might have provided refugia for zooplankton. In contrast, in the 40 g/L treatments, the absence of fish removed predation pressure, rendering the presence or absence of macrophytes less influential on zooplankton community structure. These observations highlight the interplay between abiotic stressors and biotic interactions in shaping zooplankton abundance and biomass across different salinity and temperature regimes.

4.1. Limitations

While the present findings provide valuable insights, they should be interpreted with caution due to several inherent limitations. Since these tanks had recently been used for previous experiments, initial conditions might have had legacy ecosystem effects. There was very limited variability among 40 g/L treatment tanks; however, moderate

variability was observed in the 4 g/L treatment tanks. These legacy effects and variability among replicates could have masked potential responses, reducing our ability to detect treatment effects clearly. Ensuring a more uniform distribution of the water column and thorough mixing of the sediment prior to the experiment could have improved homogeneity and reduced this variability. Some samples on certain dates contained no zooplankton, so counts from preceding or subsequent sampling dates were used to compensate. Careful fixation and collection could help prevent such sampling errors. In the 4 g/L mesocosms where fish were present, potential grazing effects on zooplankton could have been assessed using fish gut contents or isotope analysis, allowing a clearer evaluation of fish influence. The experiment was conducted over only four sampling dates in the fall; a longer-term or summer experiment with more frequent zooplankton sampling may reveal additional responses. Additionally, current warming was moderate, and stronger warming treatments could potentially induce clearer effects on zooplankton communities.

CHAPTER 5

CONCLUSION

In this study, shallow Mediterranean lakes were simulated using mesocosms to investigate the effects of salinization and warming on zooplankton communities. A clear shift in community structure was observed between low (4 g/L) and high (40 g/L) salinity treatments. In the 40 g/L mesocosms, species richness and Shannon diversity were lower, while abundance was generally high and dominated by the salinity-tolerant rotifer *Brachionus plicatilis*. In contrast, the 4 g/L mesocosms supported higher species richness, with rotifers co-occurring alongside cladocerans and copepods despite lower abundance. These results indicate a shift from diverse assemblages under low salinity to a less diverse, rotifer-dominated system under high salinity, confirming our first hypothesis that salinization favors tolerant species but may reduce energy transfer efficiency. While warming alone had limited direct effects, it may exacerbate salinity stress, suggesting that the interactive effects of temperature and salinity critically shape zooplankton abundance, biomass, body size, and community composition. These findings have important implications for understanding and managing shallow Mediterranean lakes under ongoing climate change and increasing anthropogenic salinization. Understanding how high salinity alters ecosystem functioning and food-web structure is therefore crucial for the sustainable management of lake ecosystems. Moreover, these results highlight the need to consider salinity-induced changes in water-quality assessments. Incorporating such insights will support the development of more effective strategies aimed at preserving ecosystem integrity.

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