# IMPACT OF TOP DOWN AND BOTTOM UP CONTROLS ON THE MICROBIAL LOOP IN TURKISH SHALLOW LAKES: SPACE FOR TIME SUBSTITUTE, MONITORING AND MESOCOSMS APPROACHES

A THESIS SUBMITTED TO
THE GRADUATE SCHOOL OF NATURAL AND APPLIED SCIENCES
OF
MIDDLE EAST TECHNICAL UNIVERSITY

BY

ARDA ÖZEN

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY
IN
THE DEPARTMENT OF BIOLOGY

SEPTEMBER 2012

Approval of the thesis:

**IMPACT OF TOP DOWN AND BOTTOM UP CONTROLS ON THE MICROBIAL LOOP IN TURKISH SHALLOW LAKES: SPACE FOR TIME SUBSTITUTE, MONITORING AND MESOCOSMS APPROACHES**

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# ABSTRACT

IMPACT OF TOP DOWN AND BOTTOM UP CONTROLS ON THE MICROBIAL LOOP IN TURKISH SHALLOW LAKES: SPACE FOR TIME SUBSTITUTE, MONITORING AND MESOCOSMS APPROACHES

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September 2012, 195 pages

Bacteria, nanoflagellates and ciliates constitute the microbial loop and it is a model of the pathways of carbon and nutrient cycling through microbial components of pelagic aquatic communities. The current study comprised of a comparative study of the microbial food web community along north to south latitudinal gradient using space for time susbtitute, monitoring and mesocosms experiments with contrasting nutrient and predation states. We investigated effect of fish predation through different zooplankton taxa on microbial loop community with in situ food web experiments in 14 lakes along north to south latitudinal gradient. The effect of seasonality was also determined by monitoring in Lakes Eymir and Mogan between 2010 and 2011. Effects of hydrology and fish through microbial community was studied in mesocosms in Lake Eymir. An implication of global warming along with eutrophication on microbial community was further explored in warmed and nutrient enriched artificial ponds during 4 months in Silkeborg, Denmark.

Our results revealed that temperature, hydrology, fish, macrophytes and seasonality affected the top down control of zooplankton and bottom up control of nutrients on microbial loop and interactions between controls and increase in these controls had a strong negative impact on the contribution and biomass of microbial loop and change the interactions within microbial community. Global warming may also effect the impact of top down and bottom up controls through increasing eutrophication, temperature, change in hydrology and zooplankton composition and in a consequence of that efficiency of microbial loop may decrease in the future warmer, drier and eutrophic conditions.

**Keywords:** Eutrophication, Global warming, Hydrology, Macrophytes**.,** Zooplankton.

# ÖZ

YUKARIDAN AŞAĞI VE AŞAĞIDAN YUKARI KONTROL MEKANİZMALARININ ÜLKEMİZ SIĞ GÖLLERİNDEKİ MİKROBİK ÇEVRİM ÜZERİNE ETKİSİ: ZAMAN YERİNE MEKAN, GÖL İZLEME VE MEZOKOZM YAKLAŞIMLARI

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Eylül 2012, 195 sayfa

Bakteri, nanoflagellatlar ve siliatlar mikrobik çevrimi oluştururlar ve pelajik sucul komünitelerin mikrobik bileşenleri aracılığıyla karbon ve besin tuzlarının çevrimini içeren bir modeldir. Mevcut çalışma, kuzeyden güneye enlemsel olarak mikrobik çevrimin farklı besin tuzu ve avlanma durumlarındaki değişimini karşılaştırmalı olarak zaman yerine mekan yaklaşımı, göl izleme ve mezokozm deneyleri ile biraraya getirmektedir. Kuzeyden güneye farklı enlemlerdeki 14 gölde, yerinde besin ağı deneyleri ile mikrobik çevrim üzerine farklı zooplankton grupları aracılığıyla balıkların etkisi araştırıldı. Mevsimlerin etkisi Eymir ve Mogan Göl'lerinde 2010-2011 yılları arasında yapılan düzenli örnekleme ile belirlendi. Mikrobiyal komünite üzerinde hidroloji ve balık etkisi Eymir Göl'ündeki mezokozmlarda araştırıldı. Ötrofikasyonla birlikte küresel ısınmanın mikrobiyal komünite üzerine etkisi Danimarka Silkeborg'taki ısıtılmış ve besin tuzu eklenmiş yapay havuzlarda 4 ay süreyle çalışıldı.

Sonuçlarımız, sıcaklık, hidroloji, balık, makrofit ve mevsimselliğin, mikrobik çevrim üzerine zooplankton yukarıdan aşağı kontrolü ve besin tuzlarının aşağıdan yukarı kontrolünü etkilediğini ve bu kontrollerdeki artışın mikrobik çevrimin biyokütlesi ve önemini olumsuz etkilediği ve mikrobik çevrim içindeki ilişkileri değiştirdiğini göstermiştir. Küresel ısınma ötrofikasyon, artan sıcaklık, hidroloji ve zooplankton kompozisyonundaki değişim ile kontrol mekanizmalarını değiştirebilir ve bunun sonucunda mikrobik çevrimin etkinliği gelecekte daha sıcak, kurak ve ötrofik koşullarda azalabilir.

**Anahtar kelimeler:** Ötrofikasyon, Küresel ısınma, Hidroloji, Makrofitler, Zooplankton.

To My Love Sare

## ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to Prof. Dr. Meryem Beklioğlu Yerli and Prof.Dr. Erik Jeppesen for their great support, supervision and understanding throughout in this study.

I would also express my appreciation to METU-DPT ÖYP programme of Turkey (BAP-08-11-DPT-2002-K120510), TUBITAK (Project no: 105Y332, 109Y181, and 110Y125) and EU-FP7- REFRESH (Grant aggrement number: 244121) for their financial supports.

Special thanks to my friends in METU Limnology Laboratory, Eti Levi, Tuba Bucak, Gizem Bezirci, Şeyda Erdoğan, Nihan Tavşanoğlu, Ayşe İdil Çakıroğlu, Deniz Önal, Nur Filiz, Jan Coppens, Korhan Özkan, Ece Saraoğlu and National Environmental Research Institute (NERI) staff for their help in the field and in the laboratory.

My sincere gratitude to my lab-mate Ayşe İdil Çakıroğlu performer the cluster analysis on the data of chapter 3 "Space for time substitute: snap shot sampling" and "In situ food web grazing experiments".

I greatly appreciate help of Assistant Professor Ceylan Yozgatlıgil and Dr. Sandra Brucet for their valuable advices on the statistical analysis.

Finally, I would like to thank my lovely wife Sare Özen for her patience and support for completing my thesis.

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# CHAPTER 1

# INTRODUCTION

## 1. 1. History of Scientific Achievments in the Research of Microbial Loop

It is rather a young field of research that history of microbial loop finds its roots in marine ecology (Pomeroy *et al.*, 1974; Williams, 1981; Azam *et al.*, 1983). It was previously thought that the role of bacteria was minimum in the productivity of oceans by the marine ecologists (Steele, 1974). Small numbers of bacteria were counted with old methods such as culturing bacteria on agar plates in seawater. Planktonic algae like diatoms were viewed as the base of the ocean food web by the marine ecologists since they were the main food source of small crustaceans (Ryther, 1969; Steele, 1974). However, these diatoms were not being able to count efficiently. Because they had relatively large cell body and they were retained on the plankton collection nets used by researchers (~ mesh size > 60 μm). Up to the 1980's, pelagic food webs were considered to be a relatively simple and composed of only 'grazing food chain', where phytoplankton was consumed by zooplankton and zooplankton in turn consumed by fish (Raymont, 1963; Sumich, 1976) (Figure 1.1-1). This short and rather linear food chain is now often referred to as the classical food chain (Landry, 1977; Carpenter *et al.*, 1985). This food chain only includes relatively large-sized (> 2 μm) phytoplankton however most zooplankton cannot directly consume small phytoplankton.

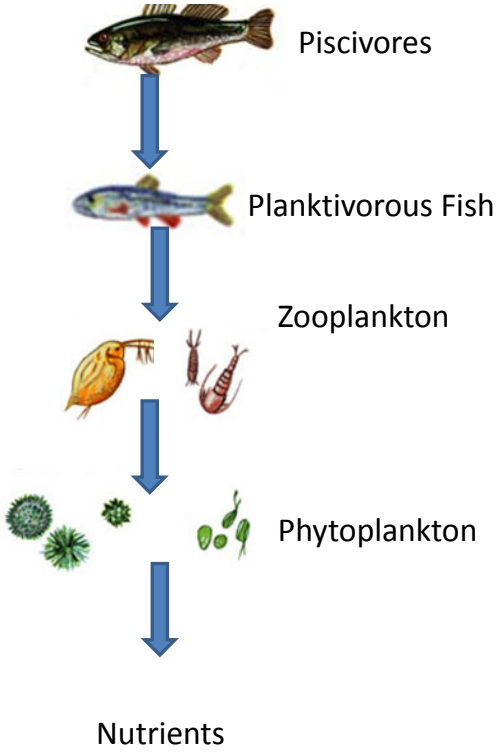


**Figure 1.1-1.** Classical food web (Taken and adapted from Molles,2010).

The higher importance of bacteria as the primary producers of oceans was lately understood by the devolopment of technology and increased research on bacteria. For example, the method of staining bacteria with a fluorescent dye and concentrating cells on a membrane filter (with pores smaller than most bacteria) yielded a better results in seawater. A highly active and dynamic microbial community was indicated by the work of Fenchel (1982,a,b,c) which made out high respiration ratios in seawater.

The paper of Pomeroy (1974) underlined the key role of microbes as a primary producers of oceans. Although there were some doubts about this paper, later studies strongly supported the Pomeroy's hypothesis (1974). In the beginning of the 1980's,

new methods based on epifluorescence microscopy were developed to study microorganisms like bacteria, picophytoplankton (< 2 μm), heterotrophic nanoflagellates (HNF) and ciliates which form the microbial food web in pelagic ecosystems (Pomeroy 1974). The term of microbial loop were coined in the paper of Azam *et al*., (1983) and pointed out that "the bacteria-consuming protists were in the same size as phytoplankton and likely an important component of the diet of planktonic crustaceans". Azam *et al.*, (1983) made a summary and connection of a new different discoveries made during the previous decade by marine biologists. It was understood that The classic view of the structure of marine plankton communities as presented by Steele (1976) was not sufficient and too simple. In this food web, bacteria and picophytoplankton are consumed by protozoa like HNF and ciliates. Zooplankton consumes these protozoa and thus links the microbial food web to the classical food chain (Figure 1.1- 2). Bacteria depend on dissolved organic matter (DOM) produced by phytoplankton. They are also grazed by protozoa and allow part of the primary production that is 'exuded' as DOM to be redirected to the classical food chain. This indirect transfer of primary production to higher trophic levels was called the microbial loop by Azam *et al*., (1983) (Figure 1.1-2). This food web also recognises the importance of viruses which induce bacterial mortality and the release of dissolved organic matter (Azam, 1998), (Figure 1.1-2).

Although the existence of bacteria and hetotrophic protists in marine environment previously had been known, their significant role as primary producers like large phytoplankton in the carbon cycle of the water column had been lately understood (Platt & Li, 1986). Counts of bacteria with new microscopic techniques were two orders of magnitude larger than the plate counts with previous counting methods. New bacteria counting techniques (Hobbie *et al.,* 1977) and usage of 14 C-labelled substrates such as glucose and amino acids, revelaed that an important part of the bacterial communities in microscopic counts was metabolically active (Wright & Hobbie, 1965, Hobbie *et al.*, 1972; Meyer-Reil,1978) and not dead or metabolically inactive cells as it previously thought. Developments such as more complex methods

for estimating *in situ* bacterial growth rates (Hagström *et al.*, 1979; Fuhrman & Azam, 1982) and a crusial role of microbes in the transformation of matter and energy in the plankton (Pomeroy, 1974) showed the important role of bacteria comparable to phytoplankton by the means of nutrient recycling in the water column (Williams, 1981; Kirchman *et al.*, 1982).

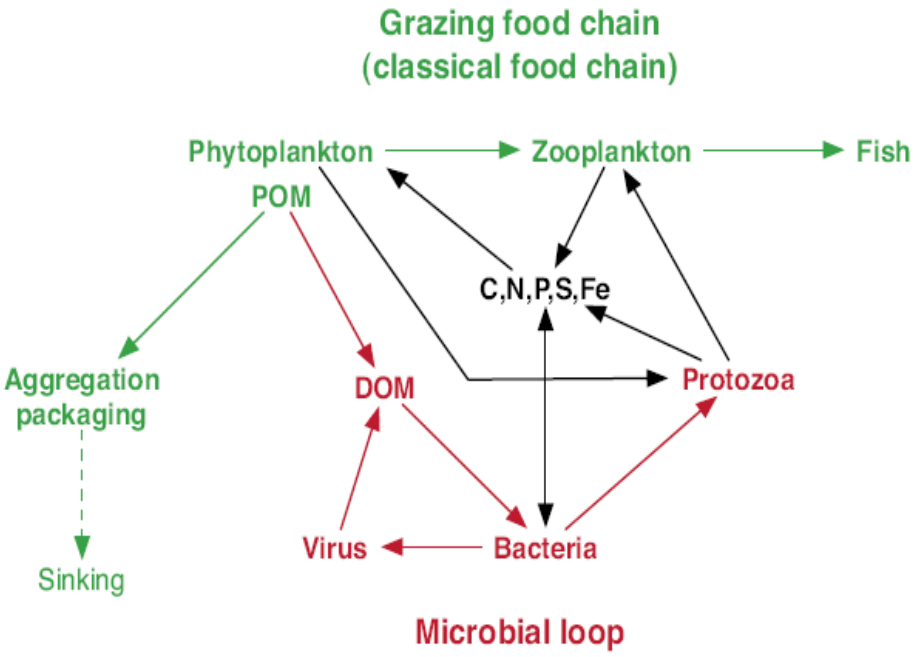


**Figure 1.1-2.** The pelagic food web highlighting the classical food chain and the microbial loop (Azam, 1998).

To understand the circumstance of the relatively important bacterial production had still remained as a problem although there were so many devolopments in this area. Since the bacteria reproduction rate fast with an average generation time of a day or less, the bacterial density usually stays relatively constant around $10^6$ cells $ml^{-1}$ in the water column. Finally, it was understood that top down controls of ciliates and flagellates are the main factor for determining the bacterial density in sea water. Functional response of bacteria and ciliate: bacteria ratios and bacteria ingestion capacity of ciliates revealed that normal concentrations of bacteria were enough to maintain populations of ciliates and flagellates. Grazing of ciliates might explain the constant density of bacteria in the water column. Fenchel (1982, a, b, c) showed the prey predator relationship between the bacteria and protozoa in long time periods studies.

The available literature was reviewed by the Azam *et al*., (1983) at that time. Crucial part of the primary production which was in the form of dissolved organic matter was lost to the environment (Fogg, 1983). Bacteria use dissolved organic matter and then protozoa graze on it and at the end, protozoa was grazed by zooplankton. A "loop" on the classic foodweb was formed by this new pathway. (Figure 1.1-2). During the years following the Azam *et al.,* (1983) paper and last two decades, different aspects of microbial community were examined in variety of studies which dominated biological oceanography,marine and freshwater systems (Fenchell, 2008). These studies clearly showed that microbial community are important components of energy flow and nutrient cycling in ocean, marine and freshwater ecosystems (Azam *et al.*, 1983, Porter *et al*., 1988; Cotner & Biddanda, 2002; Pomeroy *et al*., 2007).

Riemann and Christoffersen, (1993) shown that "the microbial food web is not a separate 'loop' but is connected to the classical grazer food chain in many direct and indirect ways by some freshwater studies". A few whole lake studies include all important components of the pelagic food web along with microbial loops (Carrick *et al*., 1991; Nixdorf & Arndt, 1993; Gaedke & Straile, 1994; Mathes & Arndt, 1994).

Less than 10% of available limnological information is focused on the organisms and metabolic processes in freshwater microbial loops (Wetzel 2000).

Most of our knowledge about the role of the bacteria in pelagic food webs mainly comes from the studies in temperate lakes and oceans. These studies revealed the vital roles of the microbial loop as a carbon source or sink in the energy flow, and for recycling of nutrients in the food web (Chisholm, 1992; Kiørboe, 1993; Williams, 2000). Although microbial components of the food web have important effects in biogeochemical flows (Cotner & Biddanda, 2002) both in oceans and freshwaters (Pomeroy & Wiebe, 1988; Weisse *et al*., 1990; Berninger *et al*., 1991; Porter, 1996; Burns & Schallenberg, 1996; Simek *et al*., 1998; Jurgens & Jeppesen, 2000), there are limited studies about composition, structure and regulation of microbial community in warm temperate and Mediterranean ecosystems (Conty *et al*., 2007). Furthermore, there are increasing interests for studies about pelagic carbon dynamics in tropical and subtropical ecosystems in recent times (Havens & East, 1997; Havens *et al*., 2000; Work *et al*., 2005; Sarmento, 2012). Thus, it is still difficult to make comparisions of microbial community among different regions due to insufficient data.

Not only phytoplankton, heterotrophic bacteria, and phagotrophic protists consist the microbial loop (Chisholm, 1988, 1992; Cambell & Vaulot, 1993) but also viruses were also important in the microbial loop (Proctor & Fuhrman, 1990; Bratbak *et al*., 1992; Thingstad *et al.*, 1993). Recent studies have showed the dynamics of virus host systems and importance of viruses for bacteria (Suttle, 1994; Suttle & Chan, 1994; Middelboe, 2000; Middelboe & Riemann, 2002; Middelboe & Jørgensen, 2006; Middelboe *et al.*, 2001).

The mortality caused by viruses which is mostly host specific is important as protozoan grazing since bacteria mostly exposed to viral attack (Fenchel *et al*., 2008).

The role of mixotrophic protists that are capable of both phagocytosis and phototrophy in microbial community lately took its place in the context of microbial loop (Estep & MacIntyre, 1989; Stoecker, 1998). It was shown that there are various types of mixotrophy: ciliates which feed on phototrophic algae, but retain their chloroplasts in a functional state for several days and can utilise the photosynthates (chloroplast retention), (Stoecker *et al*., 1989; Jones, 1994) and dinoflagellates and certain stramenopiles flagellates which control chloroplasts and are at the same time phagotrophs (Margulis, 1981). But it is sometimes difficult to differentiate this control (a chloroplast or a green symbiont). Havskum and Hansen, (1997) showed that "Such mixotrophs may make an important contribution to energetics of the water column".

The definable role of the microbial loop was largely documented with the development of new methods for estimating protozoan grazing rates, *in situ* growth rates and growth activity of bacteria (Kirchman *et al*., 1982; Fuhrman & Azam, 1982; Andersen & Fenchel, 1985; Sherr & Sherr, 1988; Sherr *et al*., 1999; Caron & Goldman, 1990; Del Giorgio & Cole, 1998) and also modelling (Thingstad, 1992; Blackburn *et al*., 1996). There were time and space impact on the role of microbial community. Although the microbial community is dominant in oligotrophic, waters, the classical planktonic food web becomes dominant in the conditions such as fresh supply of nutrients during the spring bloom in temperate waters and in upwelling areas in the ocean. Small organisms gain advantage of competition for dissolved mineral nutrients. Thus, primary production is mostly based on mineral nutrients regenerated in the water column (Chisholm, 1992; Kiørboe, 1993).

The microbial loop can be a sink by representing a loss of fixed carbon to the ecosystem or link by channeling fixed carbon to higher levels of the foodweb (Ducklow *et al*., 1986; Sherr *et al*., 1987). Thus, it was discussed whether it was a sink or link for a long time. But now, there is a general agreement that the microbial loop is basically a sink (Williams, 2000). Most of the organic carbon is used up as

$CO_2$ along the microbial loop process. Fenchel (2008) stated that "Accelerating mineralisation and regeneration production in nutrient limited systems was the central role of the microbial loop on element cycling in the water column".

### 1.2 Nutrient Cycling and the Role of Microbial Loop

Fundamental concepts in nutrient recycling were revisedby the description of the "microbial loop" (Pomeroy, 1974; Azam *et al*., 1983). Before the definition of microbial loop, it has been thought that all primary production passes through from phytoplankton to zooplankton and at the end to fish (Steele, 1974). It was lately understood that this thought was too simple and misleading as it showed by the researchs in last 20 years. It is now shown that nearly 50% of phytoplankton production may simply bypass the traditional food chain and directly pass through a complex "microbial loop" in which nutrients are rapidly recycled (Berman, 1990; Fenchel, 1988; Pomeroy & Wiebe, 1988; Sherr & Sherr, 1991) (Figure 1.2-1). As a result of the activity of, microbial communities, nutrient cycling can enhance and strong positive feedback links can introduce to the base of the food web.

The role of aquatic bacteria is very important for the cycling elements such as carbon, nitrogen and phosphorous through the ecosystem. Organic matter produced by the phytoplankton and zooplankton is converted into inorganic matter by microbial loop. This inorganic matter is used by the phytoplankton for primary production and/or photosynthesis. The production of carbon and the regeneration of nutrients are strongly influenced by the food web interactions at the microbial level (Sherr & Sherr 1987; Capblancq 1990; Weisse 1991). Phytoplankton and bacteria primarily produced of new particulate matter in pelagic systems by autotrophy and heterotrophy. The base of grazing food chains and the microbial loop was represented by the carbon pool of phytoplankton and bacteria. Cho and Azam (1990) pointed out that "the relative dominance of each functional component has significant implications for food web structure and the function and biogeochemistry of nutrients in aquatic systems".

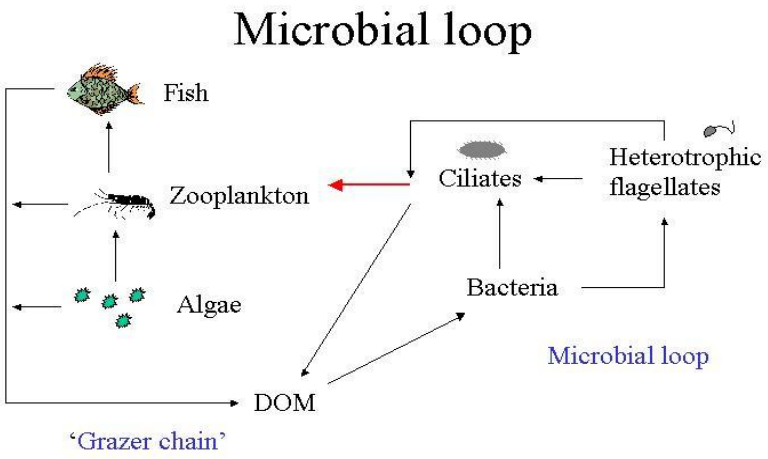


**Figure 1.2-1.** Nutrient recycling between classical food web and microbial loop.

The transfer of carbon and nutrients between the environment and autotrophs and heterotrophs provides knowledge about biogeochemical cycling and ecosystem functioning and how they interact with each other. There are two trophic pathways: the herbivorous or classical food web and the microbial loop. But Legendre & Rassoulzadegan (1995) now acknowledged that "The existence of a continuum of trophic structures with the herbivorous food web and the microbial loop as end members or connectors." Seasonality or any disturbance may affect this continuum which may result with changes in nutrient usage of community. Similarly, the Redfield ratio, (C: N: P) (Redfield *et al.*, 1963), was questioned. Coupling of carbon and nutrients has been temporaly deteriorated after bloom events (Engel *et al.*, 2002; Wetz & Wheeler 2003). For example, C: N ratio and transparent carbon-rich exopolymeric particles (Alldredge *et al.*, 1995) increase in the temporal aggregating of dissolved organic matter (DOM) (Duursma 1961; Sondergaard *et al*. 2000). Sterner & Elser (2003) pointed out that "The decoupling of carbon and nutrient cycling at the community level is related to the different abilities of autotrophs and heterotrophs to maintain homeostasis" and to the different dynamics of the

particulate and DOM pools (Banse 1994). Nelson and Carlson (2008) revealed that "Phosphorus enrichment, but not nitrogen enrichment, produces rapid and sustained increases in bacterial production rates and produces significant alterations to bacterial community structure".

Sterner and Elser (2003) claimed that "In all organisms, the carbon and nitrogen cycles are closely linked), but the coupling between carbon and nitrogen economy in heterotrophs (bacteria and higher trophic levels) and algae differs in many respects". Higher basic nitrogen demand of bacteria for proteins and nucleic acids and a lower C: N ratio of bacteria than that of most algae are these different respects. The relation between heterotrophs and algae for stoichiometric ranges for C and N are not well matched but regulated by physiological condition of heterotrophs. The carbon and nitrogen acquisition between algae and heterotrophs must be coordinated to maintain the growth but not necessarily coupled in time, and the C: N ratio of algae can be completely variable. The carbon acquired by photosynthesis is used for nitrogen assimilation by algae during the day and biosynthesis during the night until the end of photosynthesis products. Heterotrophs need the products produced by the algae for growth although they are not directly dependent on light intensity like phytoplankton. Higher trophic levels gain their energy from algae either directly (grazers) or indirectly (predators).

The importance of the microbial food web compared with the 'classical' food web is still a debatable issue in different systems. Bird & Kalff, (1984) suggested that "The primary production is used by the microbial web to a higher extent in oligotrophic lakes compared to eutrophic ones". Porter *et al*. (1998) pointed out that "The relative importance of the microbial web decreases with increasing trophic status that nutrient recycling within the microbial web is of less significance at high nutrient loadings in eutrophic lakes". Lake productivity can influence the role of the microbial loop within the food web (Bird & Kalff, 1984; Riemann & Søndergaard, 1986; Weisse, 1991b; Cotner & Biddanda, 2002) and with seasonality (Weisse & Muller, 1998).

Traditionally, scientists viewed the microbial food web as primarily a site of remineralization, supplying nitrogen and phosphorus for use as nutrients by phytoplankton. Indeed, this is one of its important functions. As it was suggested by Pomeroy *et al.,* (2007) that "Assimilation of inorganic elements into organic matter by archaea and photosynthetic bacteria and its transfer via protozoans to metazoans is also significant".

Elser *et al.,* (1990) showed that "Protistan grazing on bacteria is also an important mechanism of nutrient regeneration, in particular, of nitrogen and phosphorus. These two elements (as well as iron and silicium) limit the growth of prokaryotic and eukaryotic autotrophs in many aquatic systems". However, Thingstad, (1998) offered that "Aquatic bacteria are better competitors for phosphorus than eukaryotic algae at low ambient nutrient concentrations". Hence, bacteria biomass can include the nutrients that are required for the growth of primary producers. However, Azam *et al*., (1983) pointed out that "Bacteria also depend on the release of photosynthetically fixed organic carbon that is overproduced during phytoplankton growth". Finally, the high bacterial affiliation to nutrients has a adverse effect on phytoplankton main source of organic carbon. The activity of the bacterivorous protists amends 'lose-lose' aspect of bacterial and algal coexistence. Simon *et al*, (1983) claimed that "Compared with eukaryotes and prokaryotes have a higher nitrogen and phosphorus concentration per volume of biomass, owing to their higher ratio of proteins and nucleic acids to total cell mass". Nutrients that are not required for growth are released by protists that graze on picoplankton cells into the environment, such as dissolved amino acids (Nagata & Kirchman 1991) and ammonium (Sherr *et al.,* 1983). Growth of both primary producers and other bacteria (Kirchman, 1994) can be stimulated by this nutrient recycling.

## 1.3 Factors that control microbial loop

### 1.3.1 Top down or Bottom up control

Although the importance of control mechanisms of pelagic food webs (top-down effects versus bottom-up) is still a debating issue, The role of control mechanisms is determined by the trophic state of the water bodies. Abundance and biomass of all organisms in the food web increase with nutrient enrichment (Pace, 1986; Berninger *et al*., 1991a), but each group can show different responce (Christoffersen *et al*., 1993; Gasol & Vaque, 1993; Jansson *et al*., 1996). Nutrient enrichment can affect the structure of the pelagic community by changing the interactions among the community components. Overall ecosystem productivity both in marine and freshwater microbial food webs are affected by the top down control of bacteria by protist grazing and bottom up control of bacteria by the availability of organic carbon and nutrients (Pace *et al*.,1994, Gasol,1994) (Figure 1.3-1).

Fenchel, (2008) pointed out that "Pelagic microbial ecosystems are characterized by a complex set of dynamic interactions between organisms. Competition for nutrients and light, commensalism between autotrophs and heterotrophic bacteria, recycling of material, cell lysis, and predation are typical processes implicated in the ecological interactions between viruses, bacteria, micro-algae, and their predators (flagellates, ciliates, and microzooplankton). Top-down (grazing), bottom- up (nutrient availability, amount of prey) controls and viral lyses are primarily responsible for microbial population structure and diversity, and they operate simultaneously rather than separately".

The important roles of heterotrophic bacteria in aquatic ecosystems have been shown in different studies after the papers of Pomeroy (1974) and Azam *et al.*, (1983). They are the principal decomposers of organic matter (Wetzel, 1982), and they are thea main food source for microorganisms at the base of the trophic web (Jurgens *et*

*al.*, 1999; Hahn *et al.*, 1999; Simek *et al*., 2001). The regulation of bacterial biomass, productivity, and community structure by nutrients (both organic and inorganic) and grazing (by single-cell and multicellular zooplankton) is thus a central issue in aquatic microbial ecology (Simek *et al*., 2001; Muylaert *et al.*, 2002).

Weisse (1991) showed that "Structural changes in the pelagic food web may result in a shift from bottom-up to top-down control of some groups, e.g. heterotrophic flagellates". Lower trophic levels are mostly affected by bottom-up control and the effect of change in top-down control is less for lower trophic levels (McQueen *et al.*, 1986; Sanders *et al.*, 1994). Porter *et al.*, (1988) emphasized that "Special attention is needed to understand the community structure, the composition of metazooplankton as potential predators on the microbial component, and the composition of the microbial components in understanding the interactions between the trophic guilds".

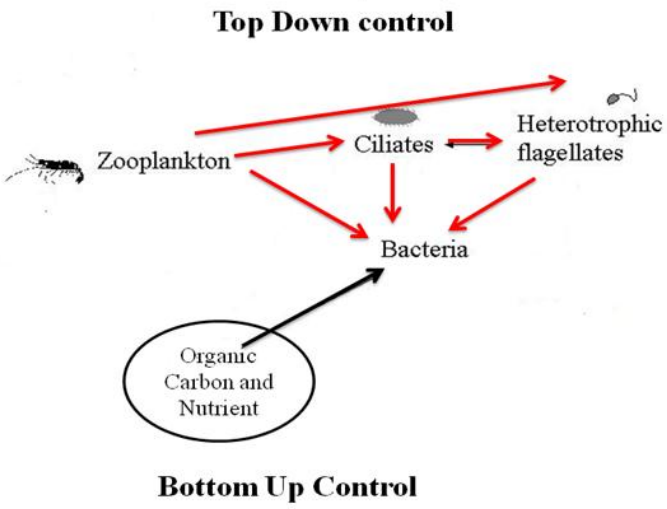


**Figure 1.3-1.** Top-down and bottom-up controls on microbial loop.

#### 1.3.1.1 Bottom up Control

Cho and Azam (1990) showed that "In pelagic systems, phytoplankton and bacterioplankton constitute the complementary functional components that primarily produce new particulate matter by autotrophy and heterotrophy. Their carbon pool represents the base of grazing food chains and the microbial loop. Thus, the relative dominance of each functional component has significant implications for food web structure and the function and biogeochemistry of nutrients in aquatic systems". An important fraction of the total planktonic biomass in pelagic systems consists of bacterial biomass and sometimes contribution of bacteria is larger than the phytoplankton contribution in oligotrophic conditions (Cho & Azam 1990; Simon *et al.,* 1992). The ratio of heterotrophic to autotrophic biomass in limnetic and marine systems declines with increasing nutrients and phytoplankton biomass (Del Giorgio & Gasol 1995; Gasol *et al.,* 1997). Algae and bacteria are are affected by continuously changing environmental conditions which have important effects on the interaction and carbon and nitrogen cycles of algae and bacteria.

Phytoplankton cells uses light energy for photosynthesis and as it shown by Baines *et al.,* (1991) "Exudates produced by phytoplankton are an important organic substrate for bacteria growth and reproduction in many aquatic ecosystems".

DOM which is the main source of bacterial carbon and the preferred source of bacterial nitrogen is the direct link from algae to bacteria (Wheeler & Kirchman 1986; Kirchman 1994). Anderson & Williams (1998) claimed that "Algae produce DOM through lysis, passive leakage, or exudation of carbon-rich material". Sources of DOM are related with algal dynamics such as enzymatic hydrolysis of particulate material through bacteria (Smith *et al.,* 1992), sloppy feeding and incomplete digestion by grazers (Jumars *et al*., 1989), and bacterial mortality after viral lysis (Cotner & Biddanda 2002). The ammonium regenerated by bacteria and higher trophic levels were used by algae for their growth. Thus, there is a relation between

the carbon and nitrogen metabolism of algae and heterotrophs but they do not necessarily go along with each others. For instance, Ducklow *et al.,* (1993) showed that "There is sample evidence that bacteria respond to increased primary production with a variable time lag of a couple of days" and also Simon and Tilzer, (1989) showed that"In spring bloom, bacterial biomass and production increases".

Thingstad *et al.,* (1998) pointed out that "As nutrient pools decrease, turnover rates and cycling through the microbial loop become increasingly important". There is strong evidence that "Food web interactions at the microbial level strongly affect the production of carbon and the regeneration of nutrients in the pelagic zone" (Sherr & Sherr 1987; Capblancq 1990; Weisse 1991). C: N: P ratio of available bacterial substrates determines the regeneration of nutrients by bacteria. Nelson and Carlson (2008) pointed out that "The metabolic and community response to nutrient enrichment by the bacterioplankton was independent of phytoplankton responses, suggesting that microbial populations may be more sensitive indicators of eutrophication and ecosystem change".

The contribution of bacterial biomass to total plankton biomass has been found higherin oligotrophic conditions (Cho & Azam 1990; Simon *et al.,* 1992). The ratio of heterotrophic to autotrophic biomass in freshwater and marine systems declines with increasing nutrients and phytoplankton biomass (Del Giorgio & Gasol 1995; Gasol *et al.,* 1997).

Development of protists and small metazoa increase in shallow eutrophic lake with large populations of inedible filamentous algae and large populations of bacteria (Porter & McDonough, 1984; Gulati, 1990; Noges *et al.,* 1998; Jeppesen *et al.,* 2000). Cyanobacterial blooms reduce the efficiency of food web in eutrophic lakes and the role of microbial pathways becomes more crucial (Gliwicz 1969; Hillbricht–Ilkowska & Havens, 1977). Work et al., (2005) showed that "Bacteria may become an important source of carbon in eutrophic lakes dominated by cyanobacteria".

Cyanobacterial toxins in limnetic food webs decline the grazing potential of larger zooplankton and inhibit the development of the sensitive protozoa (Christoffersen, 1996). In the study of Christoffersen *et al.*, (2002), it was found that "Bacteria can efficiently degrade microcystins (MCs) in natural waters with a previous cyanobacterial history, and heterotrophic nanoflagellates respond quickly to the bacterial growth". In a study by Moustaka *et al.*, (2006) in Lake Costaria (Greece), "In summer and autumn, toxic cyanobacterial blooms developed, and the microbial loop was weak. Because the heterotrophic nanoflagellates and nanociliates decreased to undetectable densities during the summer, when larger bacterivores (rotifers and small cladocera) were abundant".

In conclusion, the availability of inorganic nutrients influences the biomass of bacteria (Toolan *et al*., 1991; Elser *et al*., 1995; Rivkin & Anderson, 1997; Smith & Prairie, 2004) and bottom-up control regulates bacterial populations in different ways. Inorganic nutrients may limit bacterial growth under oligotrophic conditions, (Chrzanowski, *et al*., 1995). Porter *et al.*, (1988) stated that "the relative importance of the microbial web decreases with increasing trophic status and that nutrient recycling within the microbial web decreased in eutrophic lakes". Weisse, (1991) stated that "Eutrophication can influence the structure of the pelagic community and may have an effect on the interactions among the community components like a shift from bottom-up to top-down control of some groups, e.g. heterotrophic flagellates".

#### 1.3.1.2 Top down Control

"Bacterioplankton are heavily grazed by a wide range of organisms such as heterotrophic and mixotrophic flagellates, ciliates, rotifers, and cladocerans" (Sanders *et al.,* 1989). "Heterotrophic nanoflagellates and ciliates, the principal bacterivores constitute the link between the microbial loop and the grazing food chain through their consumption by metazoan plankton" (Callieri *et al.,* 2002).

Heterotrophic nanoflagellates are mainly responsible for bacterial biomass control (Fenchel 1982; Pernthaler *et al.,* 1998; Sanders *et al.,* 2000; Callieri *et al.,* 2002; Adamczewski *et al.,* 2010). Some studies have also pointed out that "ciliates (Jurgens *et al.,* 2000; Kisand *et al.,* 2000; Simek *et al.,* 2001), metazoans such as *Daphnia* and copepods (Adrian *et al.,* 2001; Degans *et al.,* 2001; Jurgens *et al.,* 2000), as well as lytic viruses (Bratback *et al.,* 1992; Proctor *et al.,* 1992) may also play key roles in structuring the heterotrophic bacterial community". The structure and composition of bacterial communities shift by the potential selective predation of protist predation on particular bacterial size classes or specific groups, as a result of (Hahn *et al.,* 1999, Hahn *et al.,* 2001, Jurgens *et al.,* 1999; Pertnhaler *et al.,* 1996).

Flagellates graze on bacterial populations and ciliates graze on flagellates. Ciliates play a significant role as consumers of small heterotrophic flagellates and pico- and nanophytoplankters, and are thus a link to higher trophic levels (Sanders *et al.,* 1989, Simek *et al.,* 1990, Sherr *et al.,* 1991, Szelag-Wasielewska & Fyda 1999; 2000; Zingel *et al.,* 2007). Ciliates may be also active bacterivores particularly in eutrophic lakes, where bacterial densities are sufficient to maintain ciliate populations (Pace 1982, Fenchel 1984, Sanders *et al*., 1985, Sherr *et al*., 1987, Christoffersen *et al*., 1990; Kisand & Zingel, 2000; Sherr & Sherr, 2002). Epstein and Shiaris (1992) found in the inshore bay waters of the USA that ciliates consumed bacteria 17 times faster on average than did flagellates. Thus ciliates and nanoflagellates may play a similar role in controlling bacteria depending on the trophic state of the aquatic ecosystems.

Top down control on the microbial level have been described for marine and limnetic ecosystems (Adrian, Wickham, & Butler, 2001; Jurgens & Jeppesen, 2000; Katechakis, Stibor, Sommer, & Hansen, 2002; Auer & Arndt, 2004; Schnetzer & Caron, 2005; Fonte *et al.,* 2011). The structure and dynamics of phytoplankton communities is influenced by zooplankton (Sterner, 1989; Muylaert *et al*., 2010). The impact of zooplankton on the microbial food web functions in two different

ways as it shown in different studies: “First, indirectly, by mediating the resource supply for bacteria via phytoplankton dynamics and accelerated DOC release due to grazing” (Jumars *et al*., 1989); second, directly, “by predation on microbial food web components, mainly the different groups of protists which fall into the prey size spectrum of most zooplankton species” (Arndt, 1993; Sanders & Wickham, 1993; Jürgens, 1994). The predation of zooplankton on microbial loop has been studied in details in recent years, and many species-specific effects of the zooplankton–protist link was shown. (Almost all zooplankton taxa, with the exception of cyclopoid copepods, show a strong predation pressure on heterotrophic nanoflagellates (HNF) (Sanders *et al*., 1994; Jürgens *et al.*, 1996).

The strong influence of communities with large cladocerans on entire microbial community have revealed the both direct and indirect consumption of cladocerans especially *Daphnia* spp. (Jurgens, 1994; Jurgens & Jeppesen, 2000; Langenheder & Jürgens, 2001; Degans *et al*., 2002). However, cladoceran may have positive effect on bacteria. They reduce top-down control on bacteria by reducing bacteriovores such as ciliates and HNF. They also reduce loss through sedimentation and enhanced retention of organic matter that is available for bacteria. In addition to this, they can graze on bacteria (Jeppesen *et al.*, 1992).

The highest negative effect on heterotrophic nanoflagellates was exerted by cladocerans during summer in lakes (Gasol *et al*., 1995). High *Daphnia* biomass cause important changes in the plankton size spectra (Tittel *et al*., 1998) and as it observed in seasonal plankton size spectrum rough in a highly eutrophic polymictic flushed lake (Gaedke *et al*., 2004).

Different studies showed that calanoid and cyclopoid copepods are efficient grazers of ciliates (Burns & Gilbert, 1993; Wiackowski *et al*., 1994; Wickham, 1995) and *Daphnia* affect the whole microbial food web (Porter *et al*., 1988; Jürgens, 1994).

“Copepods select for larger particle size than cladocera, thus suppressing ciliates and releasing heterotrophic nanoflagellates from ciliate predation” (Sommer *et al*., 2003).

Microcosm experiments in sub-Antarctic lakes (Tranvik *et al*., 1997) indicate “a negative effect of copepods on the abundance of heterotrophic flagellates, most probably due to grazing effect. The decrease in flagellates was concurrent with a positive effect on bacterial abundance. In the Sub-antarctic Lakes there are no cladocerans in the water column and copepods constitute the highest trophic level that is quantitatively important in food web interactions”. “Also, the calanoid copepod *Boeckella dilatata* suppressed ciliate populations in the ultraoligotrophic Lake Wakatipu in New Zealand” (Burns & Schallenberg, 1998). Burns and Schallenberg (2001) futher pointed out “those calanoid copepods were clearly more effective per unit biomass than cladocerans in removing protozoa from lakes of different productivity”. Therefore, predation by zooplankton appears to play an important role in structuring microbial food webs. On the other hand, “cyclopoid copepods had little or no effect on ciliates in eutrophic Lake Okeechobee” (Havens & Beaver, 1997), but had strong effects in mesotrophic Schöhsee (Wickham1998) and a hypertrophic lake in Denmark (Jürgens *et al*., 1999). “Differences in methods, experimental design, and data analysis reduce to the extend which the results can be compared and the generalized conclusions can not be drawn” (Burns *et al*., 2001).

There have been few studies that compare the grazing effects of cladocerans and calanoid copepods on microbial food webs. Studies of Burns and Schallenberg, (1996) and Adrian and Schneider-Olt, (1999) showed that “the negative effect of copepods on ciliates was much stronger than that of *Daphnia*” in their studies of the short-term effects of *Daphnia* and calanoid copepods on protozoa in mesotrophic lakes in New Zelandand and Germany. In contrast *Daphnia* rosea was as effective as the copepod, *Diaptomus novamexicanus* in depressing ciliate growth in a short-term study in Castle Lake, California (Wiackowski *et al*., 1994).

However, “the interaction between small-bodied zooplankton and the microbial food web is not as well known” (Ventella *et al*., 2002). According to some studies (Jurgens, Arndt & Zimmermann, 1997; Marchessault & Mazumder, 1997) “Small zooplankton can not control bacteria and protozoa”. However, Jack and Gilbert (1993) found that “most ciliates were as susceptible to *Bosmina longirostris* (O.F. Muller) as to the much larger *Daphnia pulex* (De Geer) and that the clearance rates of *Bosmina* on most ciliates were higher than its reported clearance rates on algae. As *Chydorus sphaericus* (O.F. Muller) is thought to feed in a similar way to *Bosmina* (DeMott, 1985), it is also possible that *Chydorus* feeds on ciliates and flagellates”. In a laboratory experiments, however, Archbold & Berger (1985) found that “*C. sphaericus* did not affect the numbers of the ciliate”.

Rotifers biomass contribution to total zooplankton biomass is important in most freshwater ecosystems and their food size spectrum includes the main microbial components. They are also known to feed on ciliates (Gilbert, 1980; Arndt, 1993; Gilbert &Jack, 1993; Weisse & Frahm, 2001), HNFs and bacteria (Arndt, 1993). Feeding of rotifers on bacteria is better understood (Starkweather *et al*., 1979; Bogdan *et al*., 1980; Boon & Shiel, 1990) than that on protozoans. “Rotifers may have a low transfer efficiency of organic carbon to higher trophic levels, but their function has to be considered as important organisms of the degradation process” (Arndt *et al*., 1993).

Grazing studies of zooplankton are important due to the important ecological function of zooplankton in energy and matter transfer in food webs. Although there were so many studies about the zooplankton grazing of phytoplankton (Lampert *et al.,* 1986; Sterner, 1989; Vanni & Temte, 1990), The studies about the zooplankton grazing on bacteria are substantially increased in recent times (Sanders *et al*., 1989; Vaque *et al.,* 1992; Hwang & Heath, 1999). Many of zooplankton species graze on both bacteria and phytoplankton in lakes (Bogdan & Gilbert, 1982; Børsheim & Olsen, 1984; Ooms-Wilms, 1997; Agasild & Nöges; 2005), a single food object was

studied in grazing experiments. Thus, there were relatively little information about top down control of zooplankton on phytoplankton and bacteria (Wylie & Currie, 1991; Kim *et al.,* 2000).

It was discussed for a long time that how zooplankton predation on protists affects the bacteria. Little and contradictory results were obtained for the top down control of zooplankton via field mesocosm studies in where zooplankton composition and biomass were manipulated: no clear changes in bacterial abundance with the manipulation of higher trophic levels (Pace & Funke, 1991; Wickham, 1998), or enhanced control of bacterial biomass with the presence of *Daphnia* (Riemann, 1985; Christoffersen *et al*., 1993). "The cascading trophic interactions which extend from the largest to the smallest organisms might be truncated at some lower level due to compensatory interactions" (Pace *et al*., 1998). However, not only predatory effects on the bacterial abundance and biomass but also bacterial community composition are crucial for determining the cascading predatory effects on bacteria. For example: abundance of bacterivorous protists increased in meso- to eutrophic lakes mesocosms experiments by the removal of zooplankton, or a shift from *Daphnia* to copepods. . As a result of this, bacterial community composition shifted to grazing-resistant bacterial morphotypes without major changes in bacterial biomass (Jürgens *et al.,* 1994, 1999).

Although there was so many data on the top down control of different zooplankton taxa on microbial community components, to make precise predictions about the structure, function and dynamics of the microbial food web in response to changes in zooplankton composition is not possible without seasonal data since structural and functional shifts in the microbial community may occur with the seasonal changes in the zooplankton composition (Jurgens *et al.,* 2000).

Certain micro-filtering cladocerans (Geller & Muller, 1981), particularly *Daphnia spp.* (Riemann, 1985) can graze on bacteria and use bacterial carbon and it observed

that there is a gap for bacteria -zooplankton links in the lack of filter-feeding cladocerans. Calanoid copepods consume bacteria (Knoechel & Holtby, 1986), but cyclopoid copepods do not (Sanders *et al*., 1989; Thouvenot *et al*., 1999). "Copepods select for larger particle size than cladocera, thus suppressing ciliates and releasing heterotrophic nanoflagellates from ciliate predation" (Sommer *et al*. 2003). "Copepod consumption of bacteria may result in considerable direct carbon transfer from bacteria to zooplankton in copepod-dominated systems" (Work *et al*., 2005).

No evidence for top-down control of bacterial community composition was observed in the turbid lakes, while grazing by ciliates and daphnids (*Daphnia* and *Ceriodaphnia*). Robustly changes the bacterial community in the clearwater lakes In eutrophic shallow lakes, the dominant substrate affects the seasonal change of bacterial community and food web structure (Muylaert *et al*., 2002). The main grazers on bacteria in aquatic ecosystems are heterotrophic nanoflagellates, but, especially in eutrophic environments, ciliates (Kisand *et al*.,2000) and rotifers (Conty, 2007) can become important predators too since the higher microbial biomass was observed in turbid lakes than in clearwater shallow lakes" (Mathes *et al*., 1994).

Although the top down effect of zooplankton on the microbial loop was well studied (Jürgens *et al.*, 1994, Jürgens & Jeppesen, 1998; Wickam, 1998; Zöllner *et al.*, 2003, 2009), relatively little is known about the impacts of fish-mediated trophic cascades on microbial loop processes (Riemann, 1985; Pace & Funke, 1991; Pace & Cole; 1994). Some studies revealed that the presence of planktivorous fish changed the biomass and composition of zooplankton (Riemann, 1985; Christoffersen *et al.*,1993), and this, in turn, affected bacterial biomass and production (Riemann, 1985; Markosova & Jezek, 1993) by altering the grazing pressure on bacteria. Even if omnivorous species can have profound effects on the trophic dynamics of communities and ecosystem processes, the effects of omnivorous fish, the most common feeding strategy of fish in warm water lakes (Fernando, 1991; Kolding,

1993; Starling *et al*., 2002), on microbial processes remain largely uninvestigated. Fish can also expend bottom up control as well as top down control through excretion and regeneration of nutrients (Vanni *et al.,* 1997; Vanni 2002). The effect of fish on both classical food web and microbial loop together was not fully and widely explored (Christoffersen *et al.,* 1993).

### 1.3.2 Seasonal Dynamics of Microbial Loop

Consideration of the seasonal dynamics of microbial communities was needed to understand the function of the microbial food web (Cleven *et al*., 2001; Höfle *et al.,* 1999; Pernthaler *et al*., 1998). "The combination and the importance as structuring forces of top-down and bottom-up controls show seasonal variations that play an important role in the structure and dynamics of the bacterial community", as demonstrated by Muylaert *et al*., (2002) for eutrophic lakes. The results of Muylaert *et al*., (2002) suggest that "The dominant substrate source in the lake (phytoplankton versus other sources determines bacterial succession". The effect of top-down control by grazers is overlapped on bottom up control by substrates in clear water lakes. Not only ciliates but also large metazoan filter feeders such as *Daphnia* and *Ceriodaphnia,* have an important role in the structuring of the bacterial community in different ways. Grazing on bacteria (direct effect), grazing on HNF (indirect effect by decreasing grazing pressure of HNF on bacteria). Clearwater state in shallow eutrophic lakes is stabilized by grazing of phytoplankton and many other feedback mechanisms. Besides these mechanisms, top down control of bacteria may stabilize the clearwater state in eutrophic shallow lakes since the organic matter degradation is determined by the composition of the bacterial community (Pinhassi *et al*., 1999; Riemann *et al*., 2000).

### 1.3.3 Impacts of Submerged plants on Microbial loop (indirect mechanism)

Although there are so many studies that focused on pelagic ecosystems, there are limited studies on the effects of the submerged and emerged macrophytes on the structure and functioning of the microbial communities (Komarkova & Komarek, 1975; Kleppel *et al*., 1980; Middelboe *et al*., 1998; Mitamura & Tachibana, 1999; Reitner *et al*., 1999; Scheffer, 1999; Theil-Nielsen & Søndergaard, 1999; Muylaert *et al*., 2003).

Macrophytes supply surface area available for microbial colonization and presence of macrophytes also make spacial variation in light, temperature, water current and nutrient conditions within and between macrophyte beds (Wilcock *et al*., 1999; Stanley *et al*., 2003).

In lakes, macrophytes have a profound effect on the microbial communities. Particularly, Wetzel and Søndergaard (1998) showed that "The aquatic plants play an important role in the location of the greatest bacterial growth in the water column". On the other hand, Stanley *et al*., (2003), pointed out that "Plants had a negative effect on the production of both bacteria and algae, probably because of an allelopathic effect of the macrophytes".

Mechanisms operating on zooplanktonin macrophyte beds are also indirectly acting on protozoan community. In a study by Christoffersen *et al*., (1993) showed that "the presence of planktivorous fish changed the biomass and composition of zooplankton in eutrophic lake and this is in turn affected microbial loop. When cladoceran dominated they controlled the biomass of phytoplankton, HNF, rotifers and bacteria. However, when fish reduced the cladoceran community microbial community developed with high HNF biomass". Since submerged plants provide refuge for *Daphnia* they had a negative effect on HNF. However, study of Jurgens and Jeppesen, (2000) showed that "when there were no macrophytes ciliate and bacteria

density are higher than macrophyte dominated". Zingel and Nöges (2008) showed that "the microbial loop is weaker in macrophyte dominated lakes and grows stronger, when a lake becomes more turbid. To a large extent, microbial community (bacteria, HNF and ciliates) depend directly or indirectly on phytoplankton as a food source". "Exudates produced by phytoplankton are an important substrate for aquatic bacteria in shallow lakes" (Kamjunke *et al*., 1997). HNF and ciliates feed on bacteria (Sanders *et al*. 1989) and small phytoplankton (e.g. Weisse 1990). Therefore, they think that the microbial loop is relatively stronger in plankton dominated lakes.

On the other hand, macrophytes have some positive effects on bacterial production. "Macrophyte-derived P and organic C stimulate bacterial production is also supported by mesocosm studies" (Christoffersen, 1998). "Small (< 1 mg $L^{-1}$ ) additions of macrophyte derived organic matter to lake mesocosms result in significantly higher bacterioplankton growth rates and P levels when compared to controls and algal additions" (Wehr *et al*., 1999). Phosphorous dynamics of lakes are changed by robust macrophyte beds. Pelagic energy flux is conversely routed from phytoplankton to the bacterioplankton.

### 1.3.4 Global Warming and Microbial loop

The world temperature is firmly increasing and temperature is predicted to increase 2–4 $^{o}$C within the next century in temperate regions (IPCC, 2007). Shallow lakes are likely to be particularly susceptible to global warming (Mooij *et al*., 2005; Kundzewicz *et al*., 2008; Jeppesen *et al*., 2009, 2011). Climate models also predict that precipitation and accordingly nutrient loading to lakes will increase in Northern Europe, warmer and drier conditions, decrease and change in precipitation will be observed in Mediterranean zone (Giorgi, 2006; Giorgi & Lionello,2008; .Paz *et al*., 2010). "High water temperature and light intensity like in Mediterranean lakes allow higher bacteria biomass and production with global warming" (Conty et al., 2007). Global warming is another factor that may affect both classical food web and

microbial communities. Combined with major changes in trophic structure, eutrophication is expected to intensify (Moss *et al*., 2003; Jeppesen *et al*., 2009, 2010). Among the effects on phytoplankton are increases in total biomass, shifts in the timing and magnitude of spring blooms and higher dominance of cyanobacteria (Jöhnk *et al*., 2008; Huber, Adrian & Gerten, 2008; Jeppesen *et al*., 2009), while for zooplankton shifts in seasonal phenology and size structure are to be expected (Gerten & Adrian, 2002; Gyllström *et al*., 2005; Jeppesen *et al*., 2010).

Savage *et al*., (2004) stated that "Many biological processes, such as growth and production rates of microbial organisms, are positively related to temperature". Thus, changes in water temperature due to global warming may exactly affect the microbial community. Stimulation of growth by temperature may not cause increase abundance due to negative effects, such as elevated predation (Rae & Vincent, 1998; Christoffersen *et al*., 2006). There were limited studies on the effects of global warming on microbial organisms. But studies of Christoffersen *et al*., (1993 and 1998) showed that "Temperature, nutrients and planktivorous fish effect the species composition, density and feeding activity of cladocerans and as a consequence indirect effects on the microbial community were observed" Global warming may also affect microbial communities through warming-induced eutrophication (Jeppesen *et al*., 2009, 2010), as this community is strongly affected by changes in trophic state (Carrick *et al*., 1991; Nixdorf & Arndt, 1993; Gaedke & Straile, 1994; Mathes & Arndt, 1994). Moreover, a shift in fish community structure towards smaller and more abundant plankti-benthivorous fish may enhance predatory control of zooplankton (Jeppesen *et al*., 2009) with cascading effects on bacteria, protozoans and small-bodied zooplankton (Porter & McDonough, 1984; Nõges *et al*., 1998; Jürgens & Jeppesen, 2000).

Christoffersen *et al*. (2006) pointed out that "It seems likely that warming may have affected the activity, and thus the production, of the microbial assemblage, without triggering a net increase in abundance due to an opposing effect of elevated grazing

from herbivorous zooplankton. Simulated increases in the nutrient supply had a significant effect on the microbial assemblage, and nutrient supply thus seems to be a much more important factor than warming. The response pattern, however, proved to be considerably more complex when examining in detail the effects of nutrient addition, as warming had a significant modifying effect when combined with nutrients (i.e. warming * nutrients interaction: warming has a eutrophicating effect)". Although Christoffersen *et al.*, (2006) revealed "no direct effects of increased temperatures on the lower trophic levels in the food web, it can be concluded that temperature changes indirectly induce changes, implying that climatic conditions are important for structuring the microbial food web. The results furthermore reveal that complex reactions occur when warming and nutrients act in combination. In consequence, global warming may possibly have pronounced effects on aquatic ecosystems if accompanied by increased nutrient loading".

### 1.3.5 Water Level Fluctuations

Leira and Cantonati, (2008) stated that "Water level fluctuations (WLF) were the decisive element of hydrology especially in shallow lakes since theyare particularly sensitive to any rapid change in water level and input. WLFs may have an overriding effect on the ecology, functioning and management of shallow lakes. Water levels in shallow lakes naturally fluctuate intra- and interannually depending largely on regional climatic conditions". Through global climate change, water level fluctuations may become as significant as nutrients on functioning of shallow lakes (Coops *et al*., 2003; Leira & Cantonati, 2008).

Shifts between the turbid and the clear, macrophyte-dominated state that is independent of nutrient enrichment and top-down effects may cause by WLF's (Wallsten & Forsgren, 1989; Blindow, 1992; Beklioglu *et al*., 2006, 2007). Water level seems to be a major factor influencing summer thermal stratification, nutrient dynamics and submerged plant development. Some studies suggested that WLF may

be a catastrophic disturbance for submerged plant communities since excessively high water level in growing season may suppress plant development and, in turn, such a lake may shift to a state associated with low vegetation development (Blindow 1992; Engel & Nichols, 1994; Blindow *et al.*, 1998). In contrast to high water levels, the growth and expansion of plants in the littoral zone deteriorate with too low water levels through ice and wave action in winter and dryness in summer (Blindow, 1992; Blindow *et al.*, 1993; Blindow *et al.*, 1998; Beklioglu *et al*., 2006; Tan, 2008). Decrease in summer water level results in lack of thermal stratification. This, in turn, enhances phytoplankton growth by continuous supply of nutrients through increased internal loading (Naselli-Flores, 2003).

"Most of the studies about WLF have been carried out in Europe and North America (c. 73%). Different group of organisms under the effect of WLFs were studied including macrophytes (18.4% of the papers), (7% of the papers), zooplankton and invertebrates (7% of the papers) and fish (7% of the papers)" (Leira & Cantonati, 2008). Furthermore, my literature search also showed that there was no study on the role of hydrology or WLF on microbial community.

Most of the efforts are focused on the changes of macrophyte area as controlled by WLF (Wallsten & Forsgren, 1989; Coops *et al*., 2003; Beklioğlu *et al*., 2006). Many different features of macrophyte biology and ecology were researched in different studies (Wagner & Falter, 2002; Imamoto *et al*., 2007). Murphy (2002) stated that "The strong response of wetland vegetation to hydrological conditions underlines their vulnerability to water-level variations resulting from regulation and climate variability". It was observed that the diversity of plant communities increases with unregulated WLF's (Wilcox & Meeker, 1991). Riis and Hawes (2002) pointed out that "Similarly, in natural non-regulated systems the species richness was much lower in lakes with inter-annual level variations than in lakes with intra-annual fluctuations. However, it was shown that WLF have strong impact on vegetated state in arid or semi-arid region shallow lakes (Gafny & Gasith, 1992, Beklioglu *et al*., 2006, Havens *et al*., 2004; Tan & Beklioglu, 2006).

Changes in macrophytes due to WLF may affect the microbial community in different ways. Change in macrophyte coverage may directly affect bacterial growth and biomass due to important role of macrophytes for the location of bacterial growth in the water column (Wetzel & Søndergaard 1998; Wilcock *et al.,* 1999; Stanley *et al.,* 2003) or "a negative effect on the production of bacteria, because of an allelopathic effect of the macrophytes" (Stanley *et al.,* 2003). However, increase in macrophytes due to low water level, may negatively affect the HNF and ciliates, because some studies showed that the microbial loop was weaker in macrophyte dominated lakes (Jurgens & Jeppesen, 2000; Zingel & Nöges, 2008).

WLF affects phytoplankton abundance, biomass, size structure, taxonomic composition, and species diversity (Noges & Laugaste, 1998; Kangur *et al*., 2003) by influencing both underwater light climate (Barone & Naselli Flores, 1994) and nutrient dynamics. Although there are so many published researches about the effect of WLF on macrophytes, it is also known that WLF can alsoaffect nutrients, sediments, and thermal stratification (Furey *et al*., 2004). The change in phytoplankton community and nutrient levels due to WLF may affect the bacterial growth and microbial community biomass since bacteria competes for nutrient with phytoplankton and also bacteria use exudates produced by phytoplankton as an important organic substrate in many aquatic ecosystems (Bratbak & Thingstad, 1985; Baines *et al.,* 1991) and the microbial community biomass change with the trophic state of lakes (Burns & Schallenberg, 2001; Muylaert *et al*., 2003; Auer *et al*., 2004).

WLF can have conceivably crucial direct environmental effects for fish communities (Sutela & Vehanen, 2008) such as loss of suitable spawning habitat (Gafny & Gasith, 1992) and shelter availability around the lake edge (Fischer & Ohl, 2005) by low water levels. Large water level fluctuations in lakes can determine the depth distribution of macrophytes and, affects fish communities indirectly (Rowe *et al*., 2003; Sorensen *et al*., 2005). However, change in fish may affect bottom up control on bacteria through excretion and regeneration of nutrients (Vanni *et al.,* 1997; Vanni 2002) and fish-mediated top down control on microbial loop processes

(Riemann, 1985; Pace & Funke, 1991; Pace & Cole; 1994).

Zooplankton biomass and species composition may be influenced by WLF (Naselli Flores & Barone, 1997; Mageed & Heikal, 2006) which affect food availability (bottom-up effects) and predation pressure (top-down effects) for microbial community. Due to size-dependent predation rates, a high predation pressure from fish may substantially affect the zooplankton assemblage favouring a selective shift from large to small bodied species and individuals (Brooks & Dodson, 1965). Ultimately, the microbial community and phytoplankton community may be influenced by both grazing and nutrient recycling by zooplankton (Arndt, 1993; Sanders and Wickham, 1993; Jürgens, 1994; Wickam, 1998; Zöllner *et al.*, 2003, 2009).

### 1.4 Scope of the study

Despite their abundance and likely importance in shallow lake ecosystems, our knowledge of the individual and interactive effects of top-down and bottom-up mechanisms on the regulation of microbial loop processes in food webs, which are naturally composed by both macro- and microorganisms, remains limited in Mediterranean climate zone as opposed to temperate and lately emerging tropical climatic zones. Furthermore, to the best of our knowledge, there has been no study undertaken on the microbial loop of Turkish lakes in relation with the controlling mechanisms.

Snapshot sampling with space for time substitute approach was conducted in 14 Turkish shallow lakes to determine varying role of bottom up and top-down controlling mechanisms changes on microbial loop of Turkish shallow lakes along the latitudinal gradient. The roles of nutrients or eutrophication as well as grazing pressure on microbial and plankton community were investigated through snap-shot sampling microbial community. The specific goals of snapshot sampling of microbial community were:

(1) to determine how microbial community changes on a latitudinal gradient from north to the south.
(2) To determine varying roles of top down or bottom up control factors in shaping microbial community structure along a latitudinal gradient.

Particular feeding modes of different zooplankton taxa, may produce different effects on the microbial community components. Therefore, in situ microbial food web experiments were conducted to determine the potential cascading effects of different zooplankton groups on microbial communities in these 14 study lakes along a latitudinal gradient. We analysed the responses of the different components of the microbial community: bacteria, HNF and ciliates, by comparing their temporal changes in the presence or absence of zooplankton. The following hypotheses were tested in the in situ experiments:

(1) Zooplankton grazing will adequately control microbial community.
(2) The absence of zooplankton will cause the increase of ciliates and HNF, thus promoting a negative top down effect on bacteria.

To fully understand the dynamics of microbial loop, we should take into consideration the seasonal and interannual changes of components of microbial community. To elucidate the role of seasonality, 2 year monitoring study was conducted to consider the annual cycle of microbial and planktonic community in Lakes Eymir and Mogan in relation to top down and bottom up control.

Water level fluctuations (WLF) naturally occur due to natural oscillations of wet/dry climates which is the characteristics of Mediterranean climate. However, such WLF can be further amplified through climate change. The major goal was to test the effect of water level fluctuation and top down control of fish in a eutophic lake separately and together on microbial community using in situ mesocosms with two

different depths with/out fish reflecting a possible water level fluctuation and top-down control.

Global warming may also another important factor for determining the role of microbial communities in the ecology of shallow lakes. To elucidate the effect of warming along with eutrophication on the microbial community at contrasting nutrient levels, we followed microbes and other plankton during a 4-month period (February - May, 2010) in 12 outdoor flow-through mesocosms in Silkeborg Denmark (Liboriussen *et al*., 2005). We tested the effects of nutrient enrichment and warming during winter (mesocosms covered by ice) to spring on the structure of the microbial and planktonic food web (Özen *et al*., inpress). Summary of the thesis objectives and methodsa can be found in Figure 1.4-1.

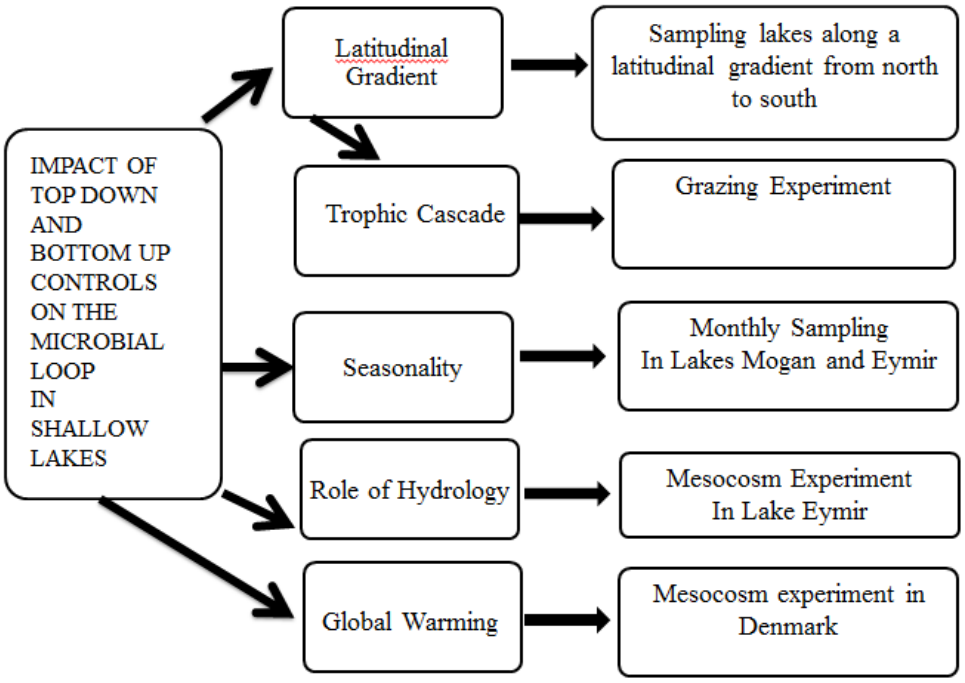


**Figure 1.4.1.** Objectives and Methods of the thesis.

# CHAPTER 2

# STUDY SITES & METHODOLOGY

## 2.1 Study Sites

### 2.1.1 Space for Time Susbtitute: Snap-shot sampling

Fourteen Turkish shallow lakes located from north to the south of the west part of Turkey between the summer of 2007 and 2010 were studied for physical, chemical and biological variables including microbial community. Each lake was sampled once during the peak of the growing season according to a well-established protocol [EUROLIMPACS (http://www.eurolimpacs.ucl.ac.uk/) and SALGA projects (http://www.projectenaew.wur.nl/salga)]. The physical, chemical and biological data excluding microbial loop, which were used in this thesis, were taken from Beklioğlu et al., (in preparation). The data set excluding microbial loop will also have been used in the PhD thesis students (Ayşe İdil Çakıroğlu, Nihan Yazgan, Eti Levi, Gizem Bezirci, Şeyda Erdoğan) who have carried out their thesis at METU, Limnology Laboratory. This study was funded by 3 TUBİTAK projects (TÜBİTAK 105Y332, TÜBİTAK 109Y181, TÜBİTAK 110Y125), OYP (BAP-08-11-DPT-2002K120510) and REFRESH (EU- FP7-ENV-2009-1). Locations, coordinates, altitudes and maximum depth of studied 14 lakes were given at Table 2.1-1.

**Table 2.1-1 Locations, coordinates, altitudes and maximum depths of studied 14 lakes. (* maximum depths of the each lake were determined during the field survey of this study).**

| Lake name | Province | Coordinates | Altitudes (m) | Maximum* depth (m) |
|---|---|---|---|---|
| Hamam | Kırklareli | 41 49 40 N; 27 57 93 E | 5 | 1.9 |
| Saka | Kırklareli | 41 48 10 N; 27 59 36 E | 1 | 2.5 |
| K.Akgöl | Adapazarı | 40 52 39 N; 30 25 57 E | 20 | 1 |
| Taşkısığı | Adapazarı | 40 52 42 N; 30 25 55 E | 27 | 3.4 |
| Poyrazlar | Adapazarı | 40 50 32,8 N; 30 28 12,3 E | 36 | 4.7 |
| Yeniçağa | Bolu | 40 46 44,7 N; 32 01 28,5 E | 988 | 4.4 |
| Gölcük | Bolu | 40 39 15,6 N; 31 37 34,6 E | 1228 | 5.2 |
| Gölcük | Kütahya | 38 16 90,3 N; 29 08 39,1 E | 1300 | 3.4 |
| Emre | Afyon | 38 06 29,7 N; 30 26 16,2 E | 1154 | 4.3 |
| Gölcük_Ödemiş | İzmir | 37 59 29,9 N; 27 19 08,0 E | 1049 | 2.5 |
| Yayla | Denizli | 38 03 118 N; 28 46 350 E | 1150 | 2 |
| Gebekirse | İzmir | 37 59 09,2 N; 27 18 14,7 E | 0 | 5.4 |
| Saklıgöl | Denizli | 37 46 644 N; 29 23 865 E | 1903 | 7.5 |
| Baldımaz | Muğla | 36 41 72 N; 28 50 063 E | 4 | 1.5 |

### 2.1.2 Monitoring of Lakes Eymir and Mogan for Microbial loop

Lakes Mogan and Eymir are two interconnected shallow lakes which were found in the Central Anatolia 20 km south of Ankara, Turkey. Semi-arid climatic conditions were observed in the region of lakes. According to data of Turkish State Meteorological Service) thirty years (1975-2006) of average air temperatures and precipitation are 21.5±0.8 ºC and 384±104 mm, respectively.

Water samples from both Lakes Eymir & Mogan were collected from January 2010 to November 2011. Samples for chemical analyses, microbial community, phytoplankton (chl-a) and zooplankton were taken biweekly intervals during the spring and summer, and monthly intervals during the winter.

#### 2.1.2.1 Lake Mogan:

It is a largeshallow lake (drainage area: 925 $km^2$, surface area: 5.4-6 $km^2$, $Z_{max}$: 3.5m, $Z_{mean}$: 2.1m, 39°47′N 32°47′ E). There are four main inflows of the lake: Sukesen, Gölcük, Yavrucak and Çölovasi brooks. The outflow runs into Lake Eymir through a canal and a wetland in the north (Figure 2.1-1).

Robust macrophyte beds exhibiting pondweed, *Potamogeton pectinatus* and *Chara* sp. were observed in lake between 1997 and 2000 by Beklioglu. Submerged macrophytes covarage ranged from 20% to 90% from 2001 to 2003 due to water level fluctuations (Beklioglu *et al.*, 2006; Tan & Beklioglu 2005, 2006). Higher levels of chlorophyll *a* and suspended solids and lower Secchi depths in 2004 resulted with low macrophyte covarage. Cyanobacteria was the dominant phytoplankton taxa and throughout the study period *Arctodiaptomus bacillifer* (Koelbel 1885) was dominant species between 1997 and2003, after 2003, rotifers became dominant taxa (Özen and Beklioglu unpublished data). Pike (*Esox lucius* Linnaeus, 1758) was dominant in the lake up to 2000 (DSI 1993; ÖÇKK 2002;

Manav & Yerli 2008). Catfish (*Siluris glanis* Linnaeus 1758) was also caught during this period.

Common carp (*Cyprinus carpio* Linnaeus 1758) and tench (*Tinca tinca* Linnaeus 1758) were the most abundant species in the lake between 2006 and 2008 and Bleak (*Alburnus escherichii* Steindachner 1897) appeared in the catches. Common carp (*Cyprinus carpio* Linnaeus 1758) and bleak (*Alburnus escherichii* Steindachner 1897) were the most abundant species in 2009. In addition, stone moroko (*Pseudorasbora parva* Temminck & Schlegel, 1846) appeared in the catches. (Fish Data for 2010 and 2011 were given in the results part.)

Ozen *et al.,* (2010) reported that "The in-lake TP concentrations were changed between 54 and 120 μg/L during the period of 1997 to 2007 and the in-lake TN concentrations were changed between 136 and 674 μg/L during the period of 1997 to 2007". 11 year mass balance study in Lake Mogan revealed that " it was only affected by natural changes (drought and water level fluctuations) in nutrient loading" It was also found that "An increase in in-lake concentrations of total phosphorus and inorganic nitrogen (ammonia as well as nitrate) occurred in dry years despite lower external nutrient loading" (Ozen *et al*., 2010).

#### 2.1.2.2 Lake Eymir

It is a small shallowlake (drainage area: 971 $km^2$, surface area: 1.20–1.25 $km^2$, $Z_{max}$: 4.3–6 m, $Z_{mean}$: 2.6–3.2 m; $39^o$, 57′ N, $32^o$ 53′ E). Most of its water receives from Lake Mogan (Eymir Inflow 1). The other inflow is Kışlakçı brook and the outflow is Eymir Out (Figure 2.1-1). Altınbilek *et al*., (1995) reports that "The lake received raw sewage effluents for more than 25 years until diversion in 1995". Beklioğlu et al., 2003 reported that "Before diversion, Inflow I constituted 89% of the total external loading of TP. The fish stock was dominated by tench and common carp in 1997-1998. To reinforce recovery after nutrient loading reduction fish biomanipulation was undertaken during 1998-1999. Fifty percent of the stock of

common carp and tench was removed and a ban on pike angling (*Esox lucius*) was introduced and had a major effect on the lake water quality: a 2-fold and 4-fold decrease in chlorophyll *a* and suspended solids, respectively, and a 2.5-fold increase in annual Secchi depth occurred". Beklioğlu and Tan (2008) reported that "Seasonal maximum coverage of submerged macrophytes was low (2.5%) before biomanipulation, but expanded after (40-90% coverage), being particularly high in the dry year 2001 due to significantly decrease in water level and increased hydraulic residence time. After the first biomanipulaton, rapid re-colonisation of submerged plants (*Potamogeton pectinatus* and *Ceratophyllum demersum*), occurred in the higher total phosphorus (TP) levels and nitrogen-limited conditions After the biomanipulation, submerged plants re-established due to reduced concentrations of TP and dissolved inorganic nitrogen (DIN)". " Ozen (2006) reported that "However, five years after the biomanipulation, the fish biomass increased again to the pre-manipulation level, and in 2004 the lake shifted back to a turbid state with scarce submerged vegetation cover and higher biomass of both tench and carp, and lower biomass of pike". The lake water quality improved (a 2-fold and 1.5-fold decrease in chlorophyll *a* and suspended solids, respectively, and a 50% increase in annual Secchi depth), but there was no major change for macrophyte coverage by the second biomanipulation between 2006 and 2007. Chlorophytes were dominant taxa during the clearwater period and cyanobacteria were the dominant taxa in the turbid period. *A. bacillifer* (Koelbel 1885) and *Daphnia pulex* de Geer were the dominant taxa from 1997 until 2003 and rotifers become dominant taxa from 2004 to 2006. Beklioğlu and Tan (2008) reported that "*Daphnia pulex* disappeared completely from the zooplankton community in 2003, probably due to increased fish predation". In 2007 the zooplankton community was characterised by dominance of *Daphnia pulex* de Geer and *Daphnia magna* Straus.

Common carp (*Cyprinus carpio* Linnaeus 1758) and tench (*Tinca tinca* Linnaeus 1758) were the most abundant species between 2006 and 2007. In addition, bleak (*Alburnus escherichii* Steindachner 1897) appeared in the catches.

Common carp (*Cyprinus carpio* Linnaeus 1758), stone moroko (*Pseudorasbora parva* Temminck & Schlegel, 1846) and bleak (*Alburnus escherichii* Steindachner 1897) were the most abundant species in 2008 and 2009. (Fish Data for 2010 and 2011 were given in the results part).

Ozen *et al*., (2010) reported that "The in-lake TP concentrations were changed between 152 and 686 µg/L during the period of 1993 to 2007.Annual mean in-lake TP concentration was 686 µg/L before sewage effluent diversion in 1995. Following effluent diversion, the in-lake TP concentration was 372 µg/L, followed by an increase during 1999, coinciding with higher hydraulic loading. After the first biomanipulation, undertaken during 1998–1999, in-lake TP decreased 372 µg/L, followed by a major increase during the low water level years (2001, 2004–2007) despite low external TP loading levels. The in-lake TP almost doubled, from 172 µg/L in 2000 to 311 µg/L in 2001 when the lake volume and water level were at their lowest. A major peak in in-lake TP of 528 µg/L coincided with an almost disappearance of submerged macrophytes Following the second biomanipulation, in 2006, when the lake volume and water level exhibited a slight increase, in-lake TP decreased markedly to 243 µg/L, but in 2007 when the water level was at its lowest and the residence time was at its highest, TP increased again to 337 µg/L".

According to the paper of Özen *et al*., (2010), "The in-lake TN concentrations were changed between 131 and 1537 µg/L during the period of 1993 to 2007. Following effluent diversion, the in-lake TN concentration decreased to 131 from 1537 µg/L. The in-lake TN concentarion decreased 1.5 fold after the first biomanipulation. However, it increased again from 2001 and onwards despite low external loading. 13 year mass balance study in Lake Eymir revealed that it was affected by natural changes in nutrient loading and it was additionally influenced by sewage diversion and restoration by fish removal. It was found that an increase in in-lake concentrations of total phosphorus and inorganic nitrogen (ammonia as well as nitrate) occurred in dry years despite lower external nutrient loading". Fish removal

changed  the in lake nitrogen concentration and water clarity, but the effect was not durable (Beklioglu & Tan, 2008; Ozen *et al*., 2010).

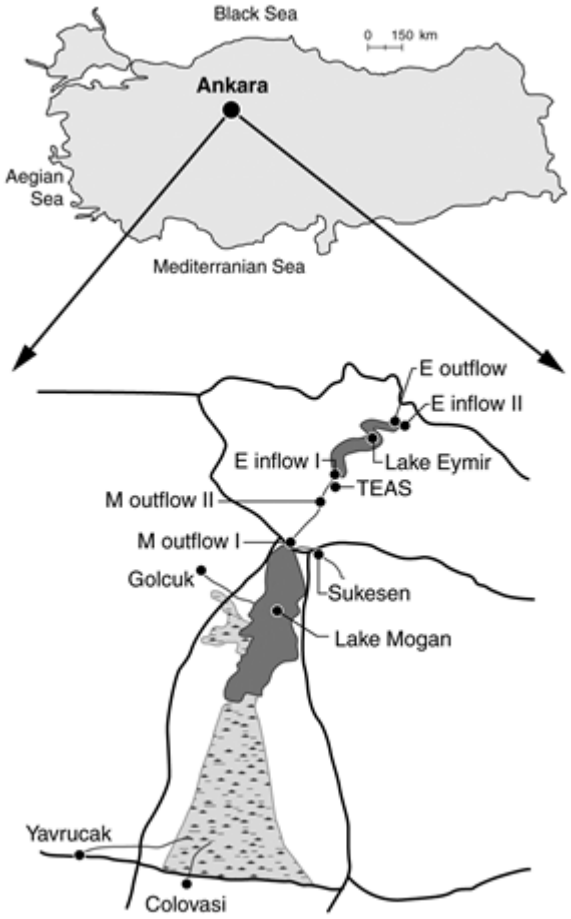


**Figure 2.1-1.** Lake Eymir and Lake Mogan (Taken from Ozen et al., 2010).

### 2.1.3 Water Level Mesocosm Experiment in Lake Eymir

The experiment was conducted in an eutrophic shallow lake Eymir from 1 June to 24 September 2009. This mesocosms experiment was designed to understand the impact of water level and fish on the growth of macrophytes as a master thesis of Tuba Bucak (2011) Bucak *et al*., (2012) and Ece Saraoğlu (2012). Mesocosms were also sampled for microbial community while the experiement was on to understand the impact of water level fluctuations and fish on microbial community.

The experiment ran at sixteen cylindrical shaped mesocosms with a diameter of 1.2 m combining two contrasting depths (low, 0.8 m- LW and high 1.6 m- HW, respectively) and the presence (+) and absence (-) of fish with four replications (Bucak *et al.,* 2012).

The mesocosms had isolating walls made of transparent polyethylene nylon with a thickness of 180 μm allowing sunlight to pass. One side of the mesocosm was attached to a circular PVC tube (diameter: 1.2 m) and kept open to the atmosphere using duct tape and cable ties, and then attached to the upper part of an aluminium frame. The bottom of the polyethylene nylon bag was attached to a circular stainless iron tube (diameter: 1.2 m) which was buried 15-30 cm into the sediment (Özkan *et al*., 2010; Bucak *et al.*, 2012). Polyurethane foam attached to the lower part of the frame ensured its buoyancy. The frame was held in place by heavy bricks at each corner. The illustration of mesocosms was given in Figure 2.1-2.

Macrophytes were removed from the sediment underneath by scuba divers using hand rakes before setting-up the mesocosms. After setting up the aluminium frame and mesocosms, they were left for a week to recover from disturbance. The dominant macrophyte in Lake Eymir, sago pondweed (*Potamogeton pectinatus* L.), was used for the experiment. Ten shoots with a length of approx. 30 cm were added to each mesocosm. Small pebbles in a plastic bag were attached to each shoot to secure them

stay in the sediment. Zooplankton collected from the lake with 50 µm plankton net were inoculated in each mesocosm. Small-sized (<10cm) tench and bleak (*Alburnus escherichii Steindachner)* (6 of each species) were stocked to half of the mesocosms, representing natural fish densities in the lake (Beklioğlu & Tan, 2008). To estimate periphyton growth, for each mesocosm eight polyethylene (PE) strips having width of 3 cm and as deep as the mesocosms were attached to a string and hung with a weight attached to the bottom of each strip.

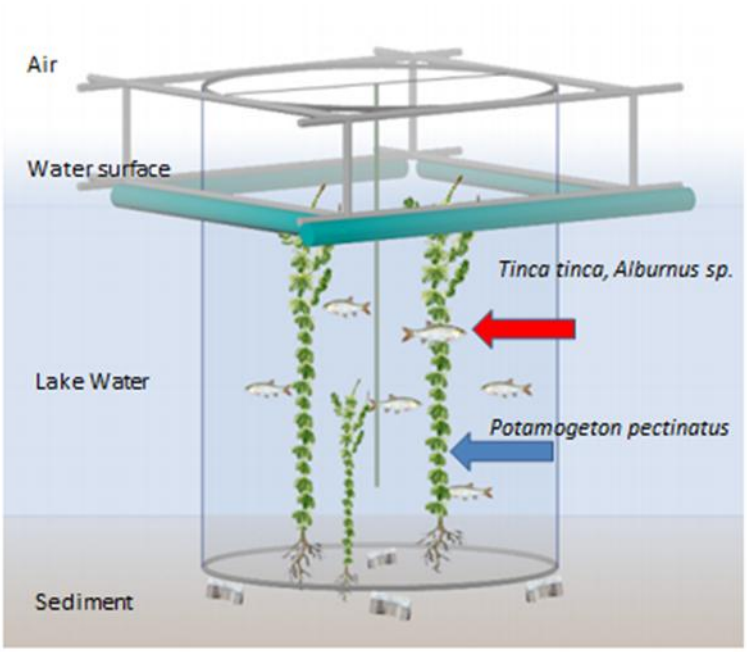


**Figure 2.1-2.** Schematic view of the enclosures; redrawn from Özkan (2008) and (Bucak, 2011).

### 2.1.4 Global Warming and Eutrophication Mesocosm Experiment (Lemming Denmark)

The mesocosm experiment was initiated in August 2003 in Lemming, Central Jutland, Denmark. It is now the longest running lake mesocosm experiment in the world. A detailed description of the mesocosms and the experimental set-up can be found in Liboriussen *et al*. (2005). It includes 24 fully mixed outdoor flow-through (tap water added several times daily, retention time ca. 2.5 month) mesocosms combining three temperature scenarios (simulating the unheated IPCC A2 scenario (Houghton *et al.*, 2001) and A2+50%) and two nutrient levels with four replications (Liboriussen *et al*., 2005). A 10 cm layer of washed sand was initially added to each mesocosm with a 10 cm layer of sediment collected from a nearby nutrient-rich freshwater pond on top. To remove large fragments of vegetation and avoid uncontrolled introduction of vertebrates such as fish or amphibians, the sediment was flushed through a net (mesh size: 1x2 cm) and drained of excess water before being placed in the mesocosms. In 2003 (first year of the study), nutrients were added weekly as $Na_2HPO_4$ and $Ca(NO_3)_2$ solutions with a constant loading of 54 mg P and 538 mg N per mesocosm each week. Depending on the results from the first year, the loading was adjusted later in the experiment between 2003 and 2010. Nutrients were added weekly to half of the mesocosms (dose: 2.7 mg P $m^{-2}$ $day^{-1}$ and 27.1 mg N $m^{-2}$ $day^{-1}$), while the rest of the mesocosms remained unenriched in the present study. Macrophytes (mainly *Elodea canadensis* Michx and *Potamogeton crispus* Linnaeus, 1753) are present in all low nutrient mesocosms, while the enriched mesocosms are dominated by phytoplankton and filamentous algae and have sparse or no vegetation. In 2003, planktivorous fish (male three-spined sticklebacks) were stocked in natural densities consistent with the nutrient treatment (Liboriussen *et al*., 2005), being 1 in the nutrient-poor and 12 fish in the nutrient-rich mesocosms. Since summer 2006, fish were allowed to breed in the high-nutrient tanks by replacing some males with females.

Not all available mesocosms were used in the present study. We randomly selected three of four replicates of the two nutrient treatments (enriched and unenriched) and two of the temperature scenarios: unheated ambient and heated, according to the IPCC climate scenario A2 scaled to local conditions in the region (average over five 25 × 25 km grid cells using a regional model [pers. comm. O. Bøssing Christensen, Danish Meteorological Institute]. Climate scenario A2 models actually predict air temperatures, but since the temperature of shallow lakes closely follows that of the air, we chose to use the modelled air temperatures as a surrogate for water temperatures. Warming was calculated as the mean air temperature increase in a particular month relative to a 30-y reference period (1961-90) and the modelled temperatures for the same month in 2071 to 2100 (Liboriussen *et al.*, 2005). The difference between the ambient and modelled temperature for the A2 scenario is generally higher in August to January (max: 4.4 °C in September) than during the rest of the year (min: 2.5 °C in June). Hereafter the treatments are termed: ambient temperature, un-enriched (A); ambient temperature, nutrient enriched (A+NP); heated, un-enriched (H); and heated, nutrient enriched (H+NP), respectively. A randomized block design was used for statistical analysis.

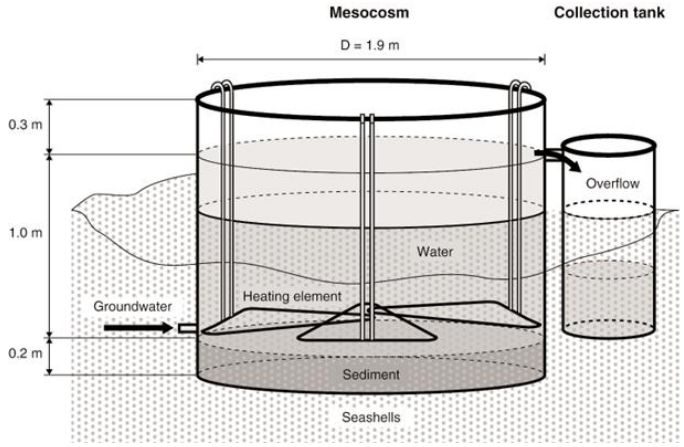


**Figure 2.1-3.** .Schematic view of one of the mesocosms and collection tank (Taken from Liboriussen *et al.*, 2005).

## 2.2. Materials & Methods

### 2.2.1 Field Sampling

#### 2.2.1.1 Space for Time Substitute: Snap-shot Sampling

A snap shot sampling protocol of EU-FP6 EUROLIMPACS (OND1304175) and SALGA projects, was applied for sampling of physical, chemical and biological variables in each lake. Lake water temperature (°C), dissolved oxygen (ml $L^{-1}$), conductivity (±1 µS $cm^{-1}$), salinity (‰), pH were determined in situ using a multi-probe meter (YSI 556 MPS, Ohio, U.S.A). Maximum depth (m) and Secchi disc transparency were measured at the deepest part of the lake using a portable sounder depth meter (Speedtech company, Virginia, U.S.A), and 20 cm diameter Secchi disc, respectively.

In each lake, 40 L of depth-integrated, water sample was collected from the entire water column at mid-lake pelagic stations located in the pelagic (deepest part) using a Ruttner type water sampler (KC- Denmark)). Water for chemical analyses of total phosphorus (TP), and total nitrogen (TN) was taken from the bulk water sample and stored in 500 mL polyethylene bottles and was kept frozen until the analysis. From the bulk water sample we took a 50 mL subsample for bacteria and HNF identification and counting, a 100 mL subsample for ciliates and a 1L subsample for Chl-a analyses.

A 20 L of bulk water sample covering the whole water column was taken using a tube sampler without disturbing the bottom from the littoral zone of lakes. From this bulk water sample we took a 50 mL subsample for bacteria and HNF analyses, a 100 mL subsample for ciliates. Twenty liter of bulk waters for both pelagic and littoral zooplankton samples were filtered through a 20 µm mesh and dispersed into a 50 mL bottle containing 2 mL acid Lugol (4% Lugol's iodine (v/v)) solution for

preservation. Before identification, each sample bottle was washed with distilled water to avoid the browning effect of Lugol.

The composition and relative abundance of the fish (Catch per unit effort - CPUE) in the lakes were determined both at pelagic and littoral using multiple mesh size Lungrens gill nets (6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60 and 75 mm in each set where mesh sizes were randomly laid). Number of set of net used was depended on the size of the lake.

Percent plant volume inhabited (% PVI) of the lakes were calculated using only submerged plant including floating leaved, floating and submerged plants data doing parallel transect lines spaced at even intervals on each lake. The numbers of transects depened on the lake area. GPS coordinates, water depth, plant species, average plant height and plant cover of each submerged and floating leaved plant species were recorded at each sampling site which are located at even intervals on each transect line. Percent PVI (%PVI) were calculated using plant surface coverage, height and water depth (Canfield *et al*., 1984). The plant samples were taken using an Ekman grab and anchor. Aquatic plants were identified using Haslam *et al.,* (1982) and Altinayar (1988).

#### 2.2.1.2 In Situ Microbial Food Web Grazing Experiments

To determine the effect of zooplankton predation on microbial food web, we conducted in situ microbial food web grazing experiments with different zooplankton structures in each of 14 lakes along north to south latitudinal gradient. In each lake, twenty litre of depth-integrated, water sample was collected from the entire water column at mid-lake stations located in the pelagic (deepest part) using a Ruttner type water sampler. Bulk water was filtered through a 20 μm mesh and filtered lake water was poured into a 1 L bottles which are the no zooplankton treatment (NZ). Large numbers of zooplankton specimens were added to zooplankton treatment bottles (Z)

together with filtered pelagic water. The experimental design consisted of 2 treatments (Z and NZ) with 6 replicates each. All bottles were placed, fixed firmly in a crate and lowered down to 1.5 m depth in littoral zone of each lake for 24 h incubation. Samples for bacteria, HNF, ciliate and zooplankton were taken before the incubation (referred initial sample) and after 24 h of incubation (referred after sample) of each experiment.

### 2.2. 1.3 Monitoring of Lakes Eymir and Mogan for Microbial loop community

Snap shot sampling procedure was applied and all parameters were sampled monthly intervals from both pelagic and littoral habitats of Lakes Mogan and Eymir.
Percent plant volume inhabited (% PVI) of the Lakes Eymir and Mogan were calculated using only submerged plant including floating leaved, floating and submerged plants data doing parallel transect lines spaced at even intervals on each lake in 2010 and 2011 using the snap shot sampling procedure.

In Lakes Eymir and Mogan, the fish density estimation was conducted once in a year when the fish were expected to be most evenly distributed and young-of the-year (YOY) large enough to be caught in the nets in 2010 and 2011 using the same nets and methods with snap shot sampling.

### 2.2.1.4 Water Level Mesocosm Experiment in Lake Eymir

Microbial loop community was sampled monthly between June and September 2009. At each sampling event, the data on water depth and percent plant volume infested (PVI%), water temperature, total phosphorus (TP), total nitrogen (TN), chlorophyll-a concentration and biomass of zooplankton community were taken from Bucak (2011) and Bucak et al. (2012).

From each mesocosm, a 4 L composite water sample integrating the whole water column was taken using a tube sampler without disturbing the bottom to determine microbial communities, including bacteria, HNF and ciliates. From the bulk water sample, we took a 50 mL subsample for bacteria and HNF analyses and a 100 mL subsample for ciliates.

### 2.2. 1.5 Global Warming and Eutrophication Mesocosm Experiment (Lemming Denmark)

All parameters were estimated monthly between February and May 2010. An 8-L water sample to determine microbial communities, including bacteria, HNF, ciliates and chlorophyll-a (Chl-*a*), was collected from the mesocosms using a 1-m long tube water sampler integrating the whole water column. We took care not to touch the plants to avoid contamination of the sample with epiphytic material. An extra sample of 8 L pooled water was taken for zooplankton analysis using the same tube sampler. In ice-covered periods (February and part of March) samples were taken through a hole drilled through the ice in the middle of the mesocosms. From the bulk water sample we took a 50 mL subsample for bacteria and HNF analyses, a 100 mL subsample for ciliates and a 1L subsample for Chl-*a* analyses. The 8 L subsample of the pooled zooplankton sample was filtered through a 50 µm mesh and dispersed into a 100 mL bottle containing 2 mL acid Lugol (4% Lugol's iodine (v/v)) solution for preservation. Before identification, each sample bottle was washed with distilled water to avoid the browning effect of Lugol.

### 2.2.2 Laboratory analysis

#### 2.2.2.1 Nutrients

Nutrient analysis of snap shot sampling, seasonal monitoring of Lakes Mogan and Eymir and mesocosm experiment in Eymir were done using the same procedures.

Total phosphorus (TP) and total nitrogen (TN) was analysed using the methods described by Mackereth, Heron & Talling (1978) and Houba, V.J.G., (1987); Kroon, H., (1993); Searle, P.L., (1984), Skalar, respectively.

Nutrient analysis of mesocosms in Denmark were determined monthly and the water was frozen prior to the analysis of total phosphorus (TP) and ortho-phosphate ($PO_4$-P) (Grasshoff, Ehrhardt & Kremling, 1983), total nitrogen (TN) (Solorzano & Sharp, 1980), and nitrate+nitrite ($NO_3$-N) using a cadmium reduction method (Grasshoff, Ehrhardt & Kremling, 1983).

#### 2.2.2.2 Bacteria and HNF

Samples for enumeration of bacteria and HNF were fixed immediately after collection by adding glutaraldehyde (Sigma, Taufkirchen, Germany) to a final concentration of 2% (v/v). Subsamples for bacteria and HNF analyses were stained for 10 min with 4'6-diamidino-2-phenylindole (DAPI, Sigma, Taufkirchen, Germany) at a final concentration of 10 µg DAPI $mL^{-1}$ (Porter & Feig, 1980). A Whatman GF/C glass microfiber filter with a pore size of 1.2 µm as a pad was used to obtain a uniform distribution of cells under low pressure (< 0.2 bar). Within 2 h following sampling we filtered the subsamples to count bacteria (2 mL) and HNF (15 mL) onto 0.2- and 0.8 µm pore size black Nuclepore filters, respectively. Filters were stored at -20 $^0$C until enumeration. The abundances of bacteria and HNF were determined by direct counting of cells using epifluorescence microscopy (Leica, DM 6000B, Wetzlar, Germany) at 1500X magnification. At least 400 bacteria cells from different fields were counted for each sample with a UV filter (420 nm). All specimens of HNF found within 1.6 $mm^2$ of each filter were counted. The microscope was equipped with a UV (420 nm) and a blue (515 nm) filter to distinguish heterotrophs from mixo- and autotrophs for HNF counting. Conversion to carbon biomass was made using a factor of 0.22 pg C $\mu m^{-3}$ for bacteria and HNF (Bratback & Dundas, 1984; Borsheim & Bratback, 1987).

#### 2.2.2.3 Measurement of bacterial production

Bacterial production was only estimated in outdoor mesocosms in Denmark.Bacterial production was estimated monthly during the study period by measuring the incorporation of [$^3$H]-thymidine into bacterial DNA (Fuhrman & Azam, 1982). We incubated 20 mL subsamples in duplicates with two 50% TCA-killed controls for 45 to 60 min (depending on the season) at the experimental treatment temperatures (control or A2 scenario) in the dark with thymidine. Incubation was stopped by adding 2 mL 50% TCA. After incubation, the samples (between 10 and 20 mL) were filtered in the laboratory onto mixed cellulose ester filters (MFS 0.2 µm, 25 mm filter diameter) and rinsed seven times with 5% TCA for 5 min. Then, we transferred the filters to plastic vials and added 7 mL scintillation liquid. The next day, we measured bacterial production in a liquid scintillation analyzer (Packard, Tricarb 1900 TR).

#### 2.2.2.4 Ciliates

Ciliates were fixed with acidic Lugol (4% Lugol's iodine (v/v)). Counting was performed in sedimentation chambers following Utermöhl (1958). Ciliates were counted under an inverted microscope with 630X magnification (Leica DMI 4000B, Wetzlar, Germany). At least 200 ciliate cells or the entire chamber were counted and identified to genus or species level according to Foissner & Berger (1996) and Foissner, Berger & Schaumburg (1999). Biovolumes of ciliates were calculated from measurements of lengths and width dimensions of animals with approximations to an appropriate geometric shape. Conversion to carbon biomass was calculated using the factor 0.14 pg C $\mu m^{-3}$ (Putt & Stoecker, 1989).

#### 2.2.2.5 Chlorophyll-*a* (phytoplankton)

For Chl-*a* concentration, 100 to 500 mL of the pelagic water samples were filtered through Whatman GF/C filters (47 mm in diameter, England). Chl-*a* was determined spectrophotometrically after ethanol extraction (Jespersen & Christoffersen, 1987).

Phytoplankton biomass was estimated using a carbon Chl-*a* ratio of 30 (Reynolds, 1984).

#### 2.2.2.6 Zooplankton

Counting of the preserved samples was performed on a 50 mL subsample at 115X magnification (cladocerans and copepods) using a stereomicroscope (Leica MZ16, Wetzlar, Germany). Rotifers were counted at 630X magnification (Leitz Labovert). Scourfield ve Harding (1966), Ruttner-Kolisko (1974), Koste (1978), Pontin (1978), Einsle (1993), Reddy (1994), Segers (1995), Smirnov (1996), Rivier (1998), Flossner (2000), Smith (2001), Ueda & Reid (2003) and Petrusek, Bastiansen & Schwenk (2005) were used to identify zooplankton.

Biomass of rotifers was calculated using standard dry weights from Bottrell *et al*. (1976) and Dumont, Van de Velde & Dumont (1975). Cladoceran biomass was calculated based on length-weight relationships from Bottrell *et al*. (1976), Dumont, Van de Velde & Dumont (1975), Culver *et al*. (1985) and Luokkanen (1995). Carbon content of zooplankton was calculated using a conversion factor of 0.48 µg C per µg dry weight (Andersen & Hessen, 1991).

### 2. 2.3. Statistical Methods

#### 2.2.3.1 Space For Time Substitute: Snap Shot Sampling

Two-way nested ANOVA was used to test differences in physical, chemical and biological variables between region and lakes. The factors were “regions” (two levels: northern and southern lakes) and “lakes” (seven levels in each region), nested within region.

Redundancy analysis (RDA) along with Monte Carlo tests (499 permutations) was performed by using the CANOCO 4.5 software (Scientia Software) (ter Braak, 1989)

to identify the relationships between environmental variables and microbial community.

Data were log-transformed before analysis to reduce skewness and to approximate to normal distribution. Before running RDA, the data were tested with detrended correspondence analyses (DCA) to evaluate suitability of the data for RDA (Ter Braak 1987). In order to reach to the highest varience, all analyses were performed with different combinations of variables and the variables which gave best results were used for the biplots. A priori forward selection of significant environmental parameters ($P < 0.05$) was performed using a Monte Carlo permutation test (499 unrestricted permutations). For the RDA, bacteria, HNF and ciliate biomass data and environmental variables which included pH, water temperature, conductivity, altitude, area, depth, dissolved oxygen, TN, TP, fish, total zooplankton, phytoplankton latitude, evaporation-precipitation and salinity from 14 lakes, among which only the 3 most influential variables (TN, water temperature, and PVI%) on species were displayed on a RDA biplots. The relation between microbial community data and explanatory variables (reduced model) was tested with a Monte Carlo unrestricted permutation test.

To identify relationships between microbial and plankton communities structure and with the independent variables TN, PVI% and temperature, stepwise multiple regression was used. Response variables in each multiple regression were the microbial and plankton communities. These statistical analyses were performed using the statistical package Systat Software, Inc. Sigma stat version 3.5.

Cluster Analysis using Euclidean distance on centered and standardized data with complete linkage was performed to group the lakes according to physical and chemical parameters and microbial community. This analysis was performed using the statistical R package. Kruskal Wallis ANOVA was performed to test differences among the biological variables between the lake clusters.

One-way ANOVA was applied in situ microbial food web experiment sets of bacteria, HNF and ciliate to control that if there was a difference between the initial treatment bottles (no zooplankton and zooplankton treatments) for each lake. Three-way nested ANOVA was used to test differences in microbial community members in *in situ* experiments between regions, lakes and treatments. The factors were "regions" (two levels: northern and southern lakes), "lakes" (seven levels in each region), nested within lakes was "grazing" (two levels: zooplankton and none zooplankton treatments). Two-way nested ANOVA was used to test differences in microbial community members in in situ experiments between lakes and treatments. The factors were "lakes", and "grazing" (two levels: zooplankton and none zooplankton treatments) nested within lakes. These statistical analyses were performed using the statistical package Minitab Software, Inc. Minitab stat version 16.

Tukey HSD pairwise comparison with 0.95 confidence level was applied to parameters having significant differences among treatments in nested ANOVA analysis. These statistical analyses were performed using the statistical package Systat Software, Inc. Sigma stat version 3.5. All data were log10 (x+1) transformed to fulfil requirements of homoscedasticity and normal distribution of residuals. Cluster Analysis using Euclidean distance on centred and standardized data with complete linkage was performed to group the lakes according to zooplankton. This analysis was performed using the statistical R package.

#### 2.2.3.2 Monitoring of Lakes Mogan and Eymir for Microbial Loop Community

To test for the effects of year and habitat over time (seasons), we used repeated measures ANOVA (RM-ANOVA) by applying SAS 9,2 software (SAS Institute Inc, Cary, NC, USA). The full data set was used for all physical (water level, pH, dissolved oxygen and temperature), chemical (salinity, water level, TP, TN and PVI %) and biological variables. Data were log-transformed before analysis to reduce skewness and to approximate to normal distribution.

#### 2.2.3.3 Water Level Mesocosms Experiments in Lake Eymir

To test for the effects of water level and fish over time (months), we used repeated measures ANOVA (RM-ANOVA) by applying SAS 9,2 software (SAS Institute Inc, Cary, NC, USA). The full data set was used for all biological and chemical (TP, TN and PVI %) variables. Data were log-transformed before analysis to reduce skewness and to approximate to normal distribution.

#### 2.2.3.4 Long-term effects of warming and nutrients on microbes and other plankton in mesocosms

To test for the effects of nutrient enrichment and warming over time (months) we used repeated measures ANOVAs (RM-ANOVAs) applying SAS 9.13 software (SAS Institute Inc, Cary, NC). The full data set was used for all biological variables. Data were log-transformed before analysis to reduce skewness and to approximate to normal distribution.

# CHAPTER 3

# RESULTS

## 3.1. Space for time substitute: snap shot sampling

Piecewise regression results showed that the $38^0$ N was the breaking point for 31 Turkish shallow lakes on a latitudinal gradient (Beklioglu *et al.*, in prep.). Lakes were grouped as northern lakes which were located above $38^0$ N and as southern lakes which were located below $38^0$ N. Furthermore, all of the physical (pH,water temperature, salinity, conductivity, water depth) , chemical (TP,TN and chlorophyll-a) and biological variables (zooplankton, fish, plant) were used in here to explain the microbial loop in these shallow lakes were taken from Beklioglu et al. (in prep. and unpublished data that resulted from 3 TUBİTAK projects (TÜBİTAK 105Y332, TÜBİTAK 109Y181, TÜBİTAK 110Y125).

Most of the lakes were freshwaters, while two lakes from the south were saline (Gebekirse and Baldımaz) with mean conductivities of 7608.8 and 5794.5 μS $cm^{-1}$, respectively (Table 3.1.1). There were not significant differences between north and south lakes and among lakes for the conductivity (Table 3.1.2).

The pH of lakes ranging from 7.2 to 9.1 in the northern lakes and 7.8 to 9.6 in the southern lakes (Table 3.1.1). There was not a significant difference between northern and southern lakes and among lakes for the pH (Table 3.1.2).

The Secchi depths of lakes ranging from 25 to 200 cm in the northern and 25 to 140 in Southern lakes (Table 3.1.1). There was not a significant difference between northern and southern lakes and among lakes for the Secchi depths (Table 3.1.2).

The mean water temperature of lakes ranging from 21.2 to 24.2 $^{o}$C in the northern and 21 to 32.2 $^{o}$C in the southern lakes (Table 3.1.1). Nested ANOVA results showed that there was a significant difference for a region effect on temperature and the mean water temperature was significantly higher in southern lakes than the northern lakes. However, among the lakes difference for temperature did not emerged as significant (Table 3.1.2). The highest water temperature was measured in southern Lake Baldımaz which was 32.2 $^{o}$C.

Total phosphorous (TP) concentrations of lakes ranging from 29 to 412 µg P $L^{-1}$ in the north and 31 to 326 µg P $L^{-1}$ in the south (Table 3.1-1). There was not a significant difference between northern and southern lakes and among lakes for the TP concentrations (Table 3.1.2).

The total nitrogen (TN) concentrations of lakes ranging from 405 to 1296 µg TN $L^{-1}$, in the north and 866 to 2028 µg N $L^{-1}$ in the south (Table 3.1.1). Nested ANOVA results showed that there was a significant difference for the regions for TN concentrations and it was significantly higher in southern lakes than the northern lakes and there was not a significant difference among the lakes for the TN concentrations (Table 3.1.2). The highest TN concentrations were measured in southern Lake Gölcük Ödemiş (2028 µg/L).

**Table 3.1-1** Physico-chemical parameters of the studied 14 lakes. Northern lakes names were written in bold (WT:water temperature).

| **Lakes** | Conductivity ($\mu S\ cm^{-1}$) | Salinity (‰) | Secchi depth (cm) | pH (log[H+]) | WT ($^oC$) | **TP** ($\mu g\ P\ L^{-1}$) | **TN** ($\mu g\ N\ L^{-1}$) |
|---|---|---|---|---|---|---|---|
| **Hamam** | 116.3 | 0.1 | 40 | 7.8 | 21.5 | 60 | 939.1 |
| **Saka** | 372.1 | 0.2 | 30 | 7.2 | 21.2 | 411.7 | 405.4 |
| **K.Akgöl** | 419 | 0.2 | 25 | 8.3 | 23.1 | 150.5 | 1296.4 |
| **Taşkısığı** | 430.5 | 0.2 | 30 | 7.5 | 23.3 | 129 | 1178.8 |
| **Poyrazlar** | 261.9 | 0.1 | 200 | 8.2 | 22.2 | 28.7 | 500.8 |
| **Yeniçağa** | 330. | 0.2 | 90 | 9.1 | 24 | 266.2 | 731.4 |
| **Gölcük_Bolu** | 168 | 0.1 | 190 | 8.5 | 24.2 | 52.5 | 613.4 |
| Gölcük Kütahya | 168.9 | 0.1 | 40 | 8.7 | 21 | 140 | 1625.8 |
| Emre | 269.9 | 0.1 | 80 | 7.8 | 23.0 | 88 | 1802.6 |
| Gölcük Ödemiş | 247.4 | 0.1 | 25 | 9.6 | 27.3 | 326 | 2028.4 |
| Yayla | 183.4 | 0.1 | 90 | 9.3 | 24 | 125 | 866.3 |
| Gebekirse | 7608.8 | 4.2 | 50 | 8.2 | 27.4 | 59.6 | 954.6 |
| Saklı | 1010.7 | 0.5 | 140 | 8 | 25.5 | 31 | 971.8 |
| Baldımaz | 5794.5 | 3.1 | 100 | 8.2 | 32.2 | 34 | 1307.7 |

**Table 3.1-2** Results of two way nested ANOVA (F-values) on the effects of region (North and South) and 'lakes' (7 lakes for each region) nested inside 'region' on some physical, chemical and biological variables of studied lakes. Significance levels:*p<0.05,**p≤0.01,***p≤0.0001, NS, none significant (p≥0.05).

| | **Region** | **Lakes** |
|---|---|---|
| Conductivity | NS | NS |
| pH | NS | NS |
| Water Temperature | 4.636 * | NS |
| Secchi Depth | NS | NS |
| TP | NS | NS |
| TN | 6.597 * | NS |
| PVI% | NS | NS |
| Fish | NS | 6.723** |
| Phytoplankton | NS | NS |

### 3.1.2 Environmental parameters and microbial loop community

There was no significant impact of region on the biological parameters and their interactions but there were significant differences among lakes (Table 3.1.3).

The relationships between the bacteria, HNF, ciliate and phytoplankton with the environmental variables were illustrated in Figure 3.1-1. RDA biplot's first two component axes explain 42.1% of total variance. Temperature was negatively correlated with first axis and positively correlated with second axis. TN was positively correlated with both axis. PVI% was positively correlated with first axis and negatively correlated with second axis. Bacteria were highly correlated with TN,

ciliates were highly correlated with PVI% whereas HNF were highly correlated with temperature.

Stepwise multiple regressions confirmed a positive relationship between bacteria biomass and TN concentrations and temperature and negative relationship with PVI% (Table 3.1-4). HNF biomass was positively related with temperature and ciliate biomass was positively related with PVI (Table 3.1-4). The HNF: bacteria ratio was positively related with temperature and negatively related with TN concentration (Table 3.1-4). Ciliate: HNF ratio was positively correlated with PVI% and negatively correlated with temperature (Table 3.1-4). Copepod: HNF, copepod: bacteria, rotifer: HNF, rotifer: bacteria, cladoceran: microbes, copepod: microbes and rotifer: microbes ratios were significantly and positively related with TN and negatively related with temperature (Table 3.1.4). The PVI% had a positive relationship with ciliate: bacteria, ciliate:HNF, rotifer:HNF, rotifer:bacteria and rotifer:microbial community ratios and negative relationship with rotifer:ciliate ratio (Table 3.1.4).

Lakes were classified with cluster analysis according to TN, PVI% and temperature since microbial community was strongly related with them according to RDA and stepwise regression analysis (Figure 3.1-6, Figure 3.1-7 and Table 3.1-4 ). To identify the differences between clusters, box plots were drawn and according to the clustering analysis, three group were characterized by a) high TN, low temperature with moderate PVI%, (1), Low TN, moderate temperature with high PVI% (2) and high TN, High temperature with no PVI% (Figure 3.1-2 and Figure 3.1-3).

Lakes were also classified with cluster analysis according to microbial community (bacteria, HNF and ciliates) and it mostly matched with dendogram of lakes according to TN, temperature and PVI%.

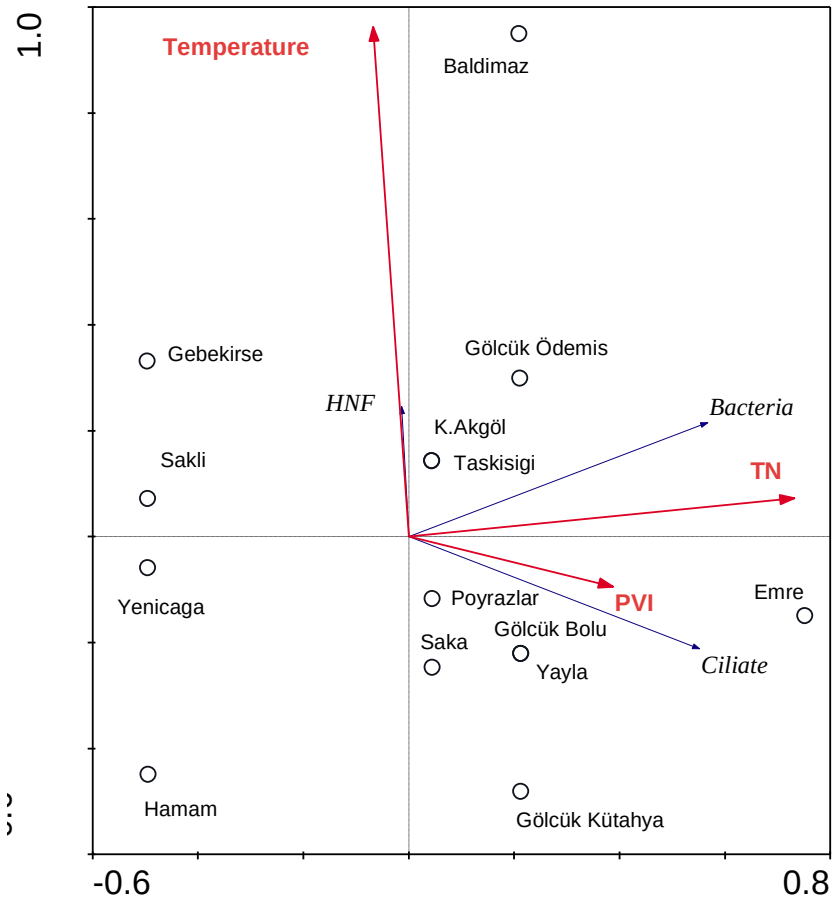


**Figure 3.1-1.** Redundancy analysis biplot showing microbial communies of 14 lakes in relation to three environmental factors, total nitrogen (TN), PVI and temperature which are indicated by gray arrows.

**Table 3.1-3** Results of two way nested ANOVA (F-values) on the effects of region (North and South) 'lakes' (7 lakes for each region) nested inside 'region'. Significance levels:*p<0.05,**p≤0.01,***p≤0.0001, NS, none significant (p≥0.05).

| | **Region** | **Lakes** |
|---|---|---|
| Bacteria | NS | 12.248*** |
| HNF | NS | 8.125*** |
| Ciliate | NS | 6.849*** |
| M.Community | NS | 12.847*** |
| Cladocera | NS | NS |
| Copepoda | NS | 18.796*** |
| Rotifera | NS | NS |
| T.Zooplankton | NS | 3.08** |
| HNF:Bacteria | NS | NS |
| Ciliate:HNF | NS | 4.292** |
| Ciliate: Bacteria | NS | 3.21** |
| Cladocera: Bacteria | NS | NS |
| Cladocera: HNF | NS | NS |
| Cladocera: Ciliate | NS | NS |
| Copepod: Bacteria | NS | 50.72** |
| Copepod: HNF | NS | 30.72*** |
| Copepod: Ciliate | NS | NS |
| Rotifer: Bacteria | NS | NS |
| Rotifer: HNF | NS | NS |
| Rotifer: Ciliate | NS | NS |
| Zooplankton: Bacteria | NS | 5.211** |
| Zooplankton: HNF | NS | 4.83** |
| Zooplankton: Ciliate | NS | NS |
| Zooplankton: Microbes | NS | 4.86** |
| Cladocera: Microbes | NS | NS |
| Copepod: Microbes | NS | 47.91*** |
| Rotifer: Microbes | NS | NS |

**Table 3.1-4** Partial correlations from the stepwise multiple regression between the microbial and plankton communities and taxonomic group with TN, temperature and PVI. Significance levels:*p<0.05,**p≤0.01,***p≤0.0001.

| | **TN** | **Temperature** | **PVI%** | **F value** |
|---|---|---|---|---|
| Bacteria | 0.063* | 0.262* | -0.311* | 0.483 |
| HNF | | 1.274** | | 0.866 |
| Ciliate | | | 0.896* | 1.285 |
| Total.Microbial Community | 0.415* | 0.124* | | 0.205 |
| Cladocera | -1.01* | | | 2.962 |
| Copepoda | | -0.75* | | 2.824 |
| Rotifera | | 1.923** | | 6.108 |
| HNF:Bacteria | -1.061** | 1.803*** | | 1.397 |
| Ciliate:Bacteria | 0.0483* | | 0.011* | 0.780 |
| Ciliate:HNF | | -0.305* | 0.148* | 1.522 |
| Cladocera:Ciliate | 0.240* | 1.410** | | 7.342 |
| Cladocera:HNF | 0.236*** | | | 1.231 |
| Cladocera:Bacteria | | 1.821*** | | 7.719 |
| Copepod:Ciliate | 0.810* | 1.620** | | 7.309 |
| Copepod:HNF | 0.570*** | -1.03*** | | 8.857 |
| Copepod:Bacteria | 0.379** | -0.560** | | 8.340 |
| Rotifer:Ciliate | 0.706*** | 2.122*** | 0.173** | 20.576 |
| Rotifer:HNF | 0.422*** | -0.078** | 0.056** | 10.347 |
| Rotifer:Bacteria | 0.244** | -0.092** | 0.046* | 3.473 |
| Cladocera:T.Microbial community | 0.944 *** | -0.917** | | 8.617 |
| Copepod:T.Microbial Community | 0.421** | -0.343* | | 7.992 |
| Rotifer:T.Microbial Community | 0.123*** | -0.035** | 0.023** | 5.448 |

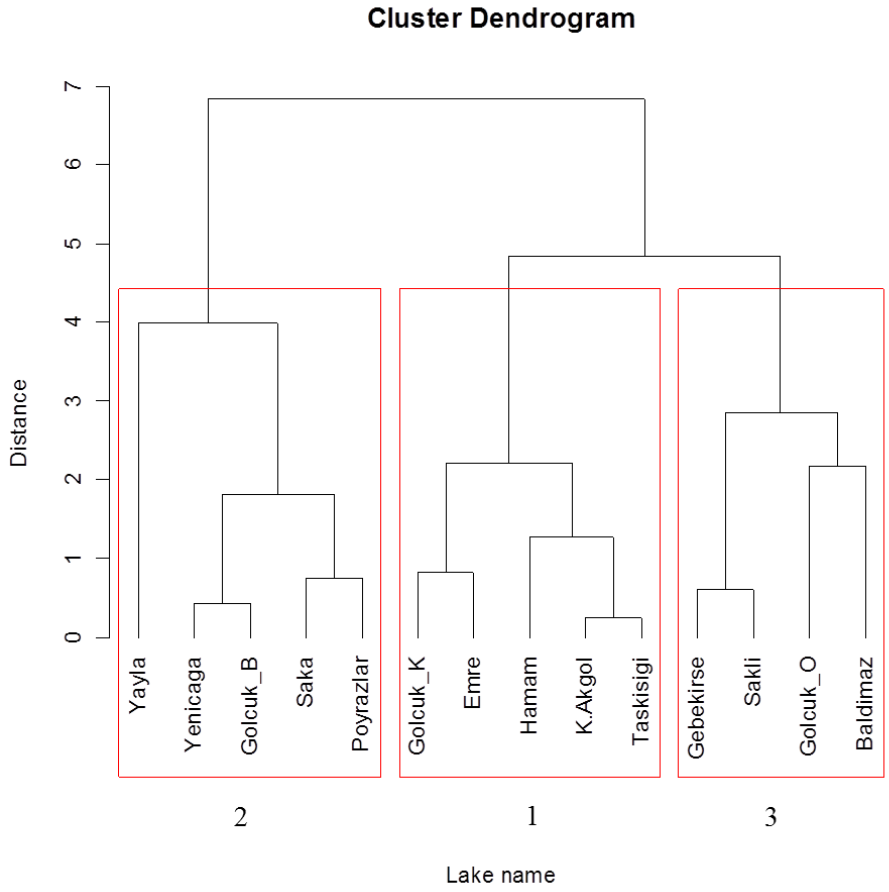


**Figure 3.1-2.** Cluster dendogram of the lakes according to TN, temperature and PVI % of 14 lakes.

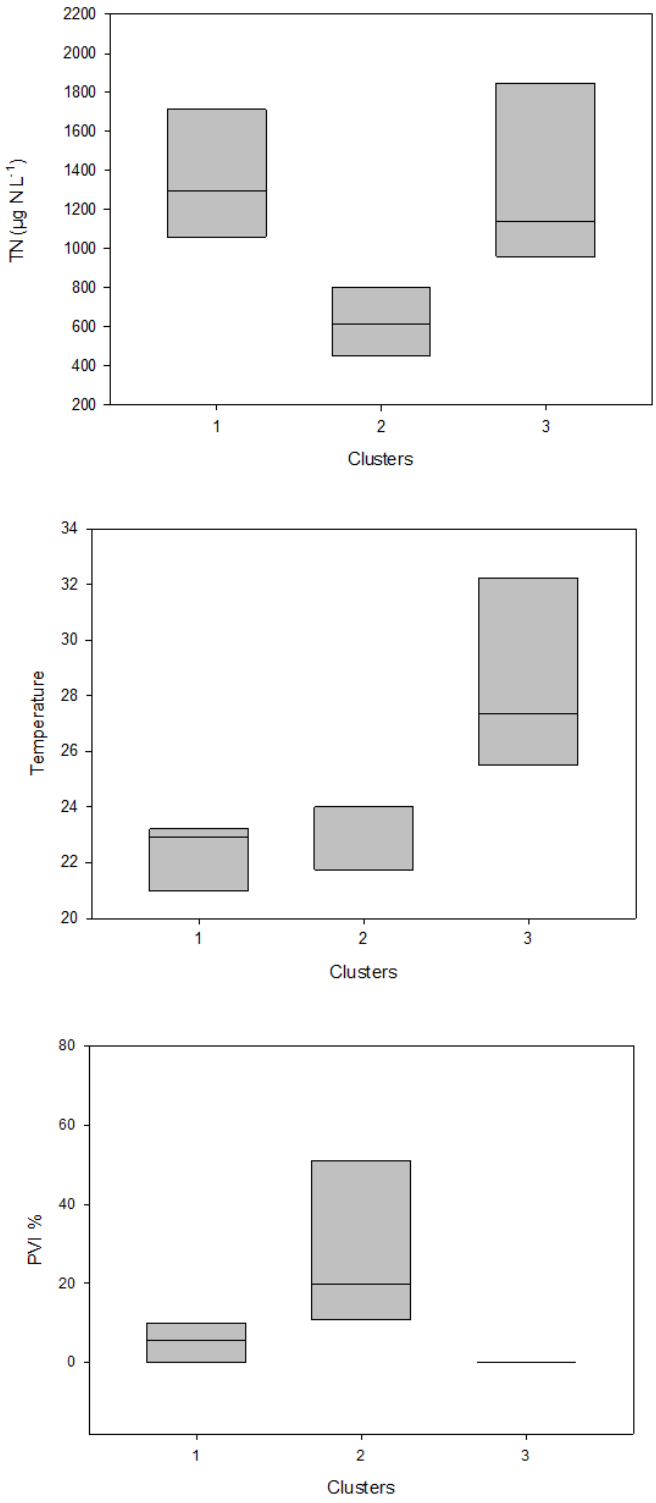


**Figure 3.1-3.** Clusters of TN, temperature and PVI% of 14 lakes.

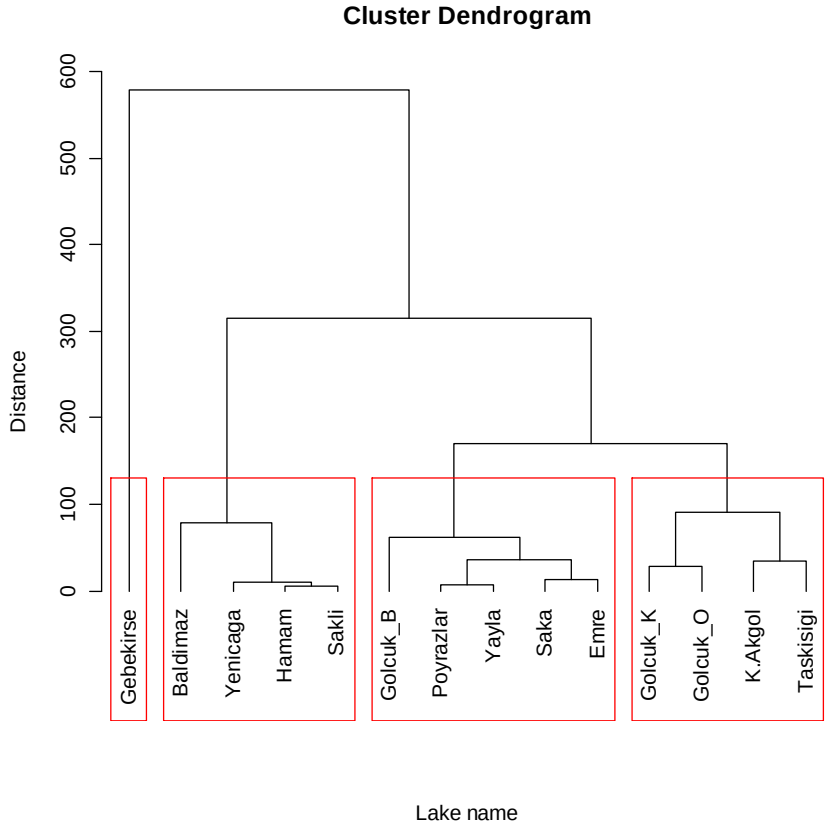


**Figure 3.1-4.** Cluster dendogram of the lakes according to microbial community of 14 lakes.

### 3.1.3. Biological parameters

**Bacteria:**

Total bacterial biomass ranged between 55 to 350 µg C $L^{-1}$ in studied lakes (Figure 3.1.5). Two- way nested ANOVA revealed that there was a significant evidence for lake effects on bacteria biomass (Table 3.1.3). Kruskal Wallis ANOVA results showed that there was significant difference among clusters (p:0.02) and lowest biomass was observed in lake cluster 2 (Tukey HSD test).

**HNF:**

Total HNF biomass ranged between 45 to 387 μg C $L^{-1}$ in studied lakes (Figure 3.1.5). There was a significant evidence for lake effects on HNF biomass (Table 3.1.3). There was no significant differences among clusters of lakes.

**Ciliate:**

Total ciliate biomass ranged between 0.5 to 13 μg C $L^{-1}$ in studied lakes (Figure 3.1.5). There was a significant evidence for lake effects on ciliate biomass (Table 3.1.3). Two- way nested ANOVA revealed that there was a significant evidence for lake effects on ciliate biomass (Table 3.1.3). Kruskal Wallis ANOVA results showed that there was significant difference among clusters (p:0.01) and highest biomass was observed in lake cluster 1 (Tukey HSD test).

Oligotrichida dominated both in northern and southern lakes and included the genera *Codonella, Halteria, , Strobilidium* and *Strombidium* and further northern lakes also had genara of *Limnostrombidium*. However, there were no ciliate in southern Lakes Saklı and Gölcük Kütahya.

**Phytoplankton:**

Chlorophyll-a concentration was used to estimate phytoplankton biomass. Mean estimated phytoplankton biomass ranged between 136 and 1876 μg C $L^{-1}$ in studied lakes (Figure 3.1.5). Two-way nested ANOVA results showed that there was no significant regional impact on the phytoplankton biomass and no significant differences among lakes (Table 3.1-2).

**Zooplankton:**

Total mean zooplankton biomass varied between 0.3 to 191 μg C $L^{-1}$ in studied lakes (Figure 3.1.5). There was a significant impact of lakes on total zooplankton biomass (Table 3.1.3).

Total cladoceran biomass ranged from 0 to 84 μg C $L^{-1}$ (Figure 3.1.5) in studied lakes. There was no significant impact of region and lakes on total cladoceran biomass.

Total copepod biomass ranged from 0.1 to 142 μg C $L^{-1}$ in studied lakes (Figure 3.1.5). There were significant lake impacts on the copepods biomass, (Table 3.1.3). Kruskal Wallis ANOVA results showed a significant differences among clusters (p: 0.03) and it was higher in cluster 2 (Tukey HSD test).

Total rotifera biomass ranged from 0.1 to 16 μg C $L^{-}$ studied lakes (Figure 3.1.5). Total rotifera biomass did not differ among regions and lakes (Table 3.1-3).

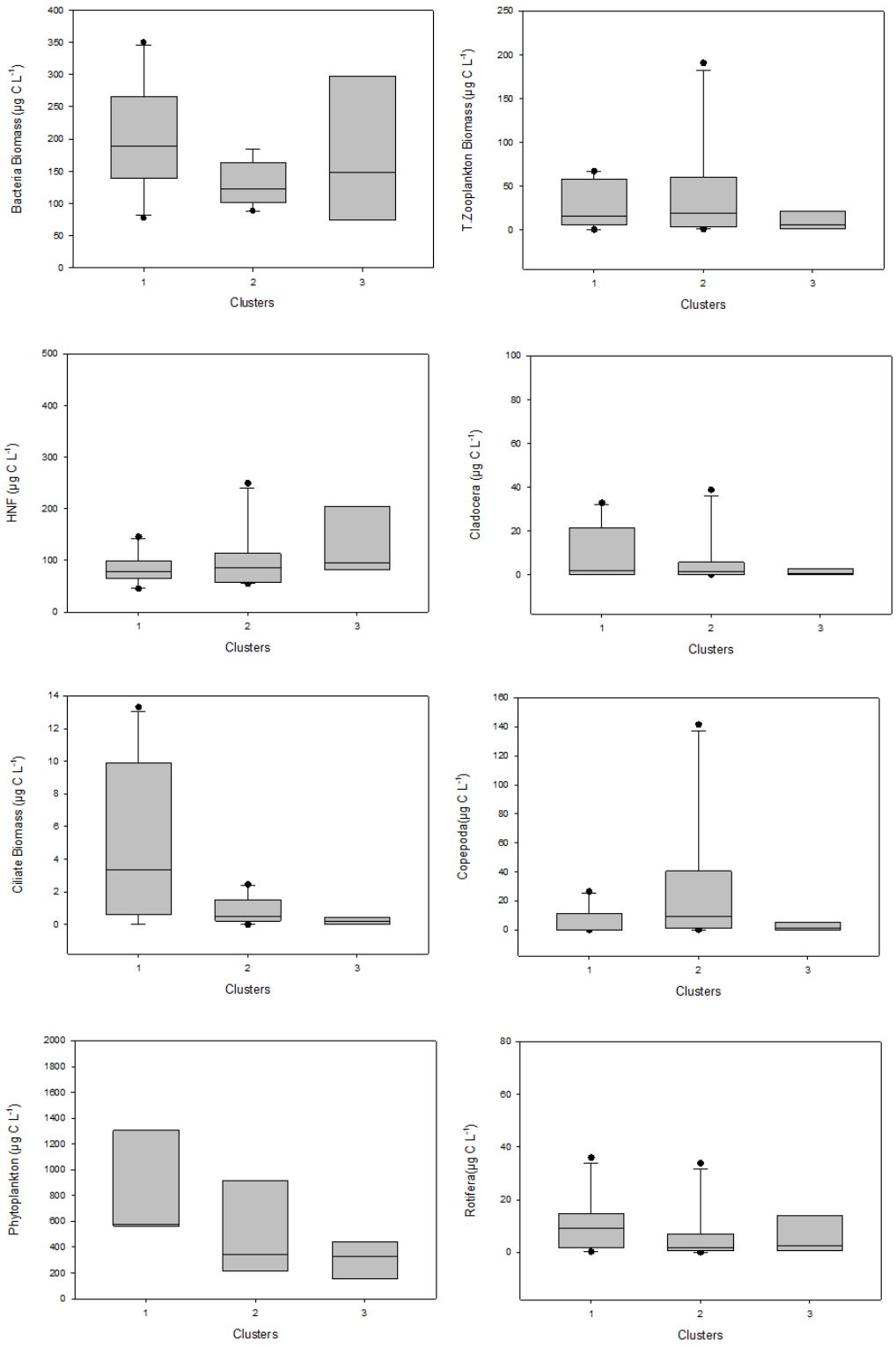


**Figure 3.1-5** Biomasses of bacteria, HNF, ciliate, phytoplankton,t.zooplankton, cladocera,copepoda and rotifera in 3 lake clusters.

**Fish:**

Most of the total planktivorous fish biomass were observed in the littoral zone (92 to 1880 g CPUE day$^{-1}$) than in the pelagic zone of Northern lakes (varied between 115 to 1589 g CPUE day$^{-1}$). Most of total planktivorous fish biomass were in the pelagic zone (varied between 33 to 1976 g CPUE day$^{-1}$) and less were in the in the littoral zone of Southern lakes (varied between 8 to 993 g CPUE day$^{-1}$) (Figure 3.1.6).

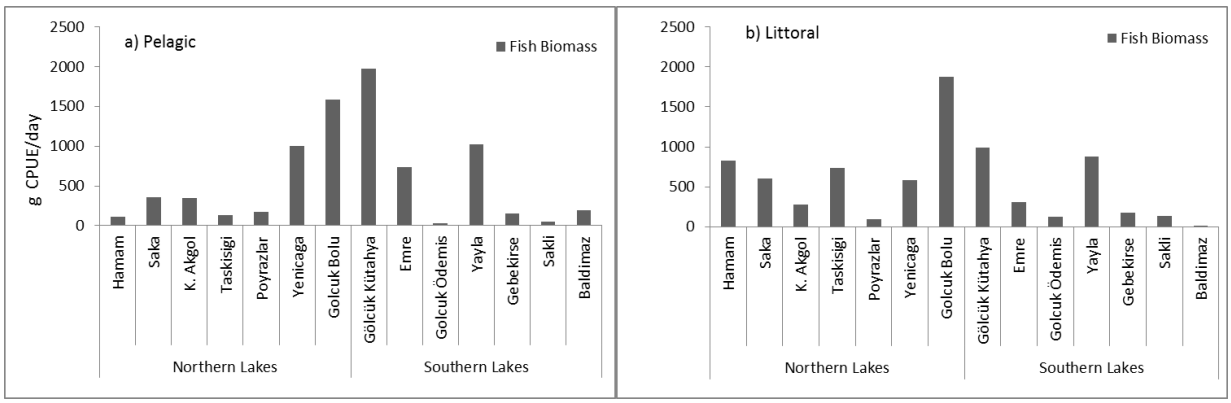


**Figure 3.1.6.** Biomasses of planktivorous fish in pelagic and littoral zone of studied 14 lakes.

**Macrophytes:**

The PVI% varied between 0 to 32 % in northern lakes and 0 to 70 % in southern lakes (Figure 3.1-7). However, rare or no submerged plant was observed in some lakes (northern lake: Taşkısığı, K.Akgöl and southern lakes: Gölcük Ödemiş, Gebekirse, Saklıgöl and Baldımaz).

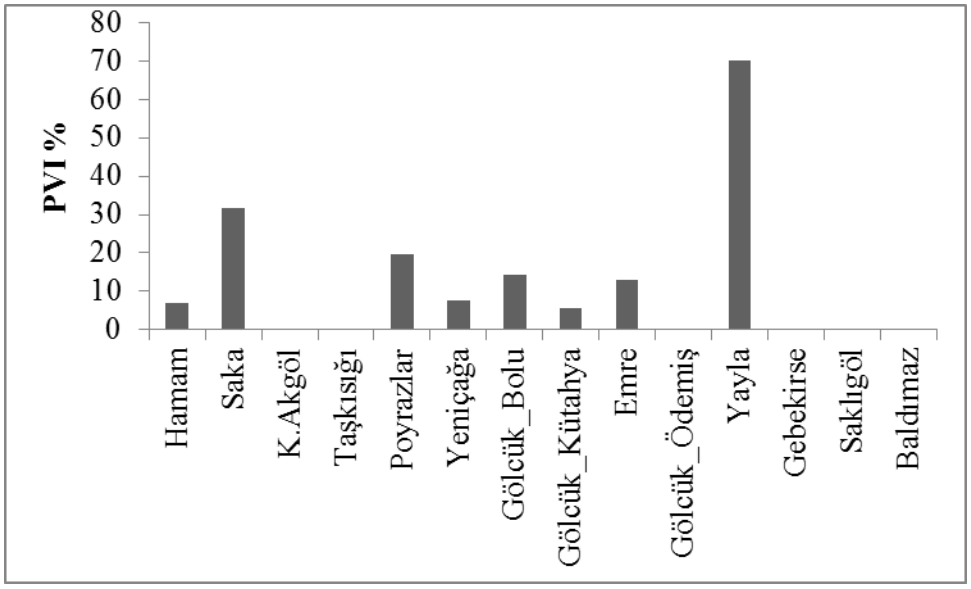


**Figure 3.1-7** Plant volume inhabited (% PVI) of studied 14 lakes.

### 3.1.4 Proportion of zooplankton, phytoplankton and microbial biomass in the pelagic zone of lakes

The contribution to total microbial biomass varied between 13 to 63 % in studied lakes. The contribution of estimated phytoplankton to total plankton biomass varied between 37 to 87 % in studied lakes. The contribution of zooplankton to total plankton biomass varied between 0.1 to 32.2 % in studied lakes.

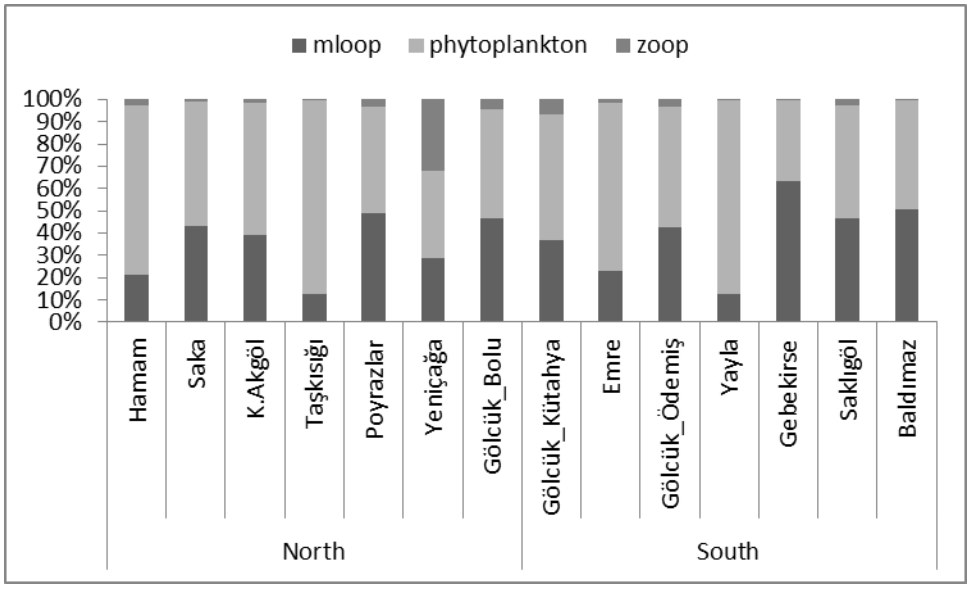


**Figure 3.1.8.** Average contribution (%) of zooplankton, phytoplankton and the sum of HNF, ciliates and bacterial biomass to total microplankton and mesoplankton biomass in the pelagic zone of studied 14 lakes.

### 3.1.5 In situ food web (grazing) experiments

The initial biomass and composition of zooplankton in zooplankton treatments were given in Table 3.1.5. Results of one-way ANOVA showed that there was no significant difference for the microbial community biomass for the initial days of treatments in each lakes.

Three-way nested ANOVA results showed that there were no regional impact on microbial communities (Table 3.1.6) and there were lake impact on only bacteria biomass (Table 3.1-6). Furthermore, three-way nested ANOVA results revealed a strong grazing impact of zooplankton on bacteria, HNF and ciliate biomasses (Table 3.1.7).

Two-way nested ANOVA was carried out for determining the effects of lakes and grazing when the region was removed as for being not significant though it yielded to the same results that the grazing impact on microbial communities (Table 3.1.7) and there was a lake impact only on bacteria (Table 3.1.7).

Lakes were classified with cluster analysis according to zooplankton community structure charcaterized by biomass since the zooplankton grazing was the treatment factor (Figure 3.1-9). To identify the differences between clusters, box plots were drawn and according to this, three group were characterized by high zooplankton biomass (1), medium zooplankton biomass (2) and low zooplankton biomass (Figure 3.1-9).

Ciliate biomasses were not changed after 24 h incubution in control bottles in all lake groups. There was no ciliate after 24 h incubation in zooplankton treatment bottles in all lake groups (Figure 3.1-11 and Figure 3.1-12). HNF biomasses were decreased in clusters 1 and 3 and decreased in cluster 2 after 24 h incubation in the control bottles (Figure 3.1.11). HNF biomasses were increased in clusters 1 and 2 and decreased in cluster 3 after 24 h incubation in zooplankton treatment bottles (Figure 3.1.12).

Bacteria biomasses were increased in all lakes clusters in control treatment after 24 h incubation (Figure 3.1.11). Bacteria biomasses only decreased in cluster 1 after 24 h incubation in zooplankton treatment bottles and there were no change in bacteria biomass in clusters 2 and 3. Two- way nested ANOVA results revealed a significant lake impact on bacterial biomass and it was significantly higher in Lake Gebekirse among 14 lakes (Tukey HSD, p:0.001).

**Table 3.1.5** Zooplankton biomass (μg C $L^{-1}$) of the in situ food web experiments carried out in 14 lakes (Names of Northern lakes were written in bold).

| | **Small Cladocera** | **Large Cladocera** | **Cyclopoid Copepod** | **Clanoid Copepod** | **Rotifera** | **Total zooplankton** |
|---|---|---|---|---|---|---|
| **Hamam** | | | 6.1±3 | | 7.3±2 | 13.5±5 |
| **Saka** | | | | | 9.7±2 | 9.7±2 |
| **K.Akgöl** | 12.7±2 | | 55±7 | | 217.7±42 | 285.3±43 |
| **Taşkısığı** | 34.9±5 | | 9.1±3 | | | 44±7 |
| **Poyrazlar** | 4.3±1 | | 4.1±1 | | 2±0.5 | 10.3±4 |
| **Yeniçağa** | 5.9±1 | 21.2±0.1 | | 25.8±4 | | 52.9±1 |
| **Gölcük Bolu** | 4.6±1 | 2±0.1 | 2.5±0.5 | | 0.1±0.01 | 9.1±0.4 |
| Gölcük Kütahya | 26.9±1 | 3.7±0.4 | 14.8±2 | | 10.2±0.4 | 55.6±3 |
| Emre | 2.3±1 | 13.8±2.7 | 0.6±0.1 | | 7.3±2 | 24±9 |
| Gölcük Ödemiş | 2±0.1 | 0.8±0.1 | 3.6±1 | | 4.2±0.1 | 10.4±0.1 |
| Yayla | 0.6±0.1 | | 1.4±0.4 | 2.3±1 | 2.2±0.2 | 6.6±1 |
| Gebekirse | | | 8.9±3 | 5.9±1 | 0.6±0.1 | 15.4±5 |
| Saklı | 2.4±0.3 | 1.6±0.2 | 6.4±1 | 2.5±0.5 | 1.5±0.1 | 14.3±2 |
| Baldımaz | | | | | 0.6±0.1 | 0.6±0.1 |

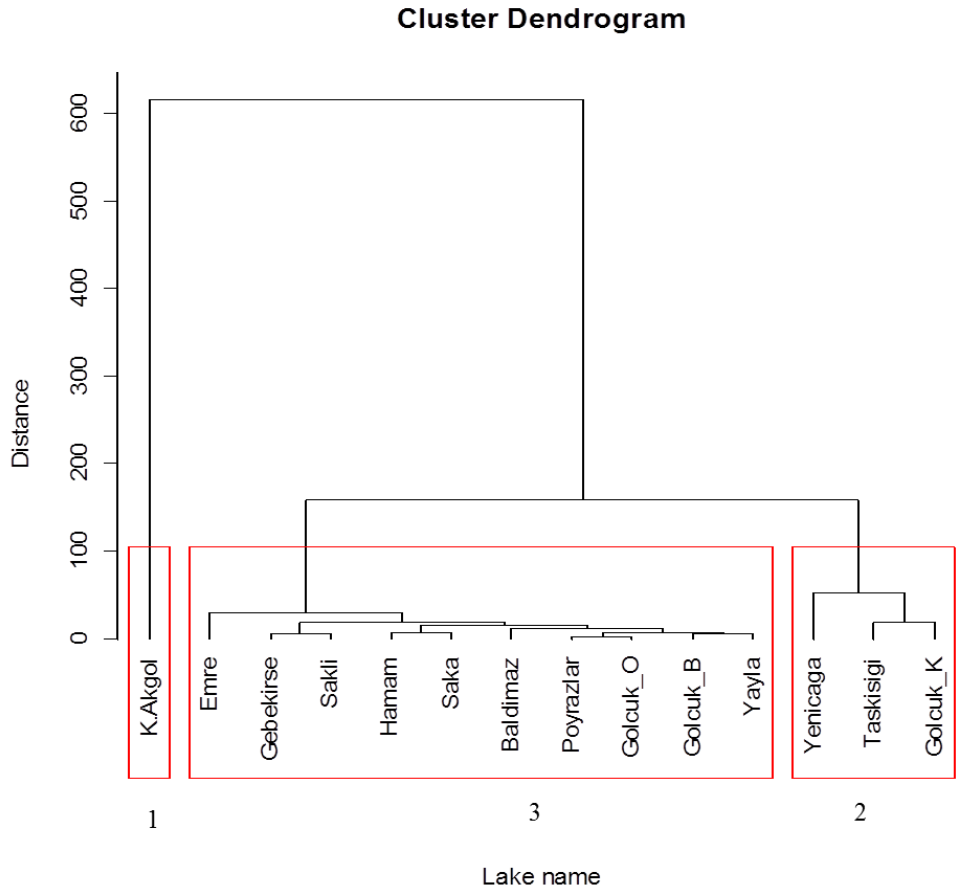


**Figure 3.1-9.** Cluster dendogram of the lakes according the zooplankton biomass of 14 lakes.

**Table 3.1-6** Results of three way nested ANOVA (F-values) on the effects of region (North and South) and 'lakes' (7 lakes for each region) nested inside 'region' and grazing (zooplankton and no zooplankton) on bacteria,HNF and ciliate. Significance levels:*p,0.05,**p,0.01,***p,0.0001, NS, none significant (p≥0.05).

| | **Region** | **Lakes** | **Grazing** |
|---|---|---|---|
| Bacteria | NS | 7.821,*** | 38.346*** |
| HNF | NS | NS | 29.816*** |
| Ciliate | NS | NS | 99.205*** |
| Ciliate:HNF | NS | NS | 78.240*** |
| Ciliate:bacteria | NS | NS | 109.472*** |
| HNF:bacteria | NS | NS | 49.398*** |

**Table 3.1-7** Results of two way nested ANOVA (F-values) on the effects of'lakes' (7 lakes for each region) ) and grazing (zooplankton and none zooplankton Significance levels:*p<0.05,**p≤0.01,***p≤0,0001, NS, none significant (p≥0.05).

| | **Lakes** | **Grazing** |
|---|---|---|
| Bacteria | 4.743* | 3.251** |
| HNF | NS | 6.661*** |
| Ciliate | NS | 27.854*** |
| Cil:HNF | NS | 25.276*** |
| Cil:B | NS | 35.874*** |
| HNF:B | NS | 13.480*** |

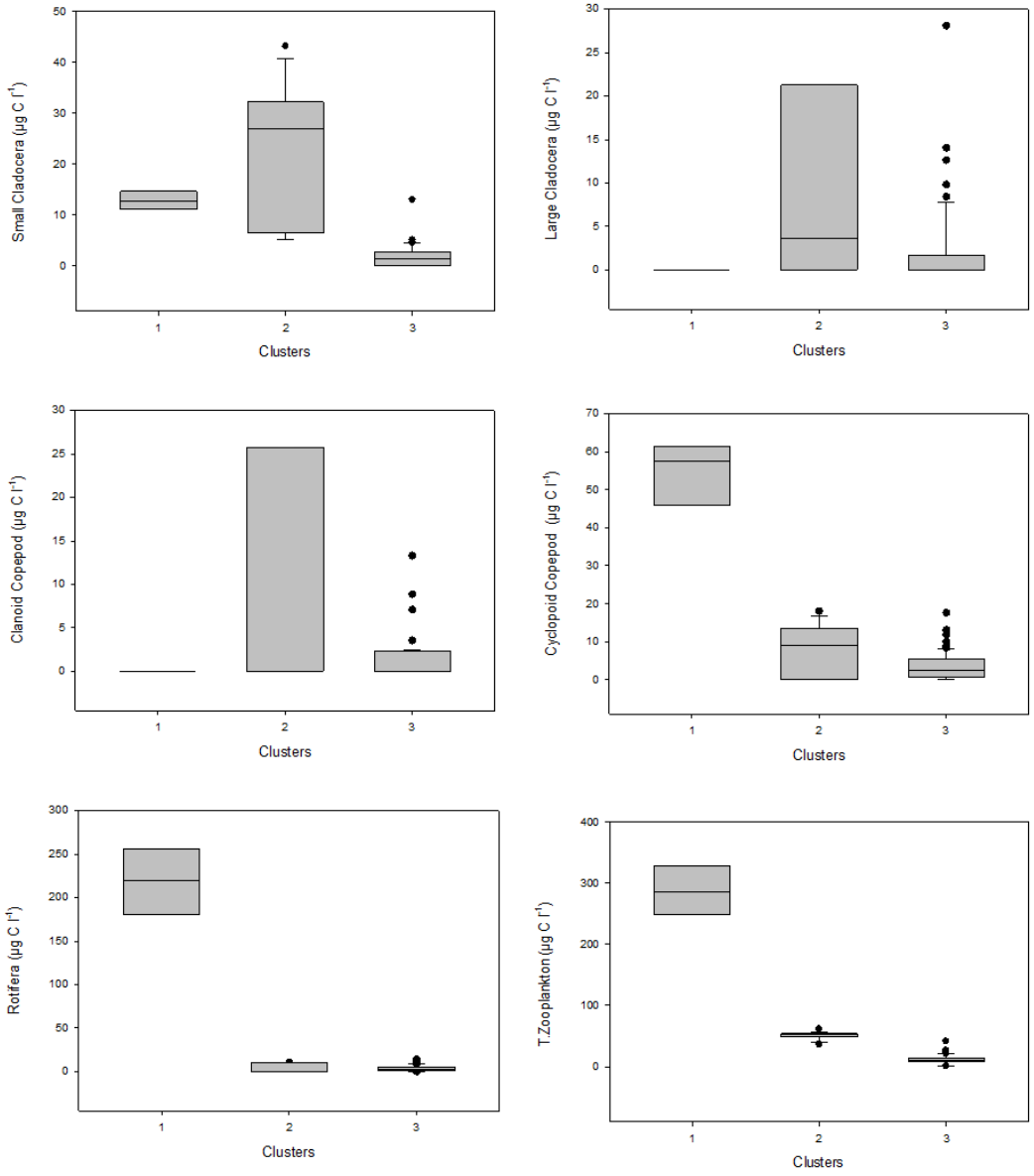


**Figure 3.1-10.** Biomass of small cladocera, large cladocera, clanoid copepod, cyclopoid copepod, rotifer and total zooplankton in clusters of zooplankton treatments.

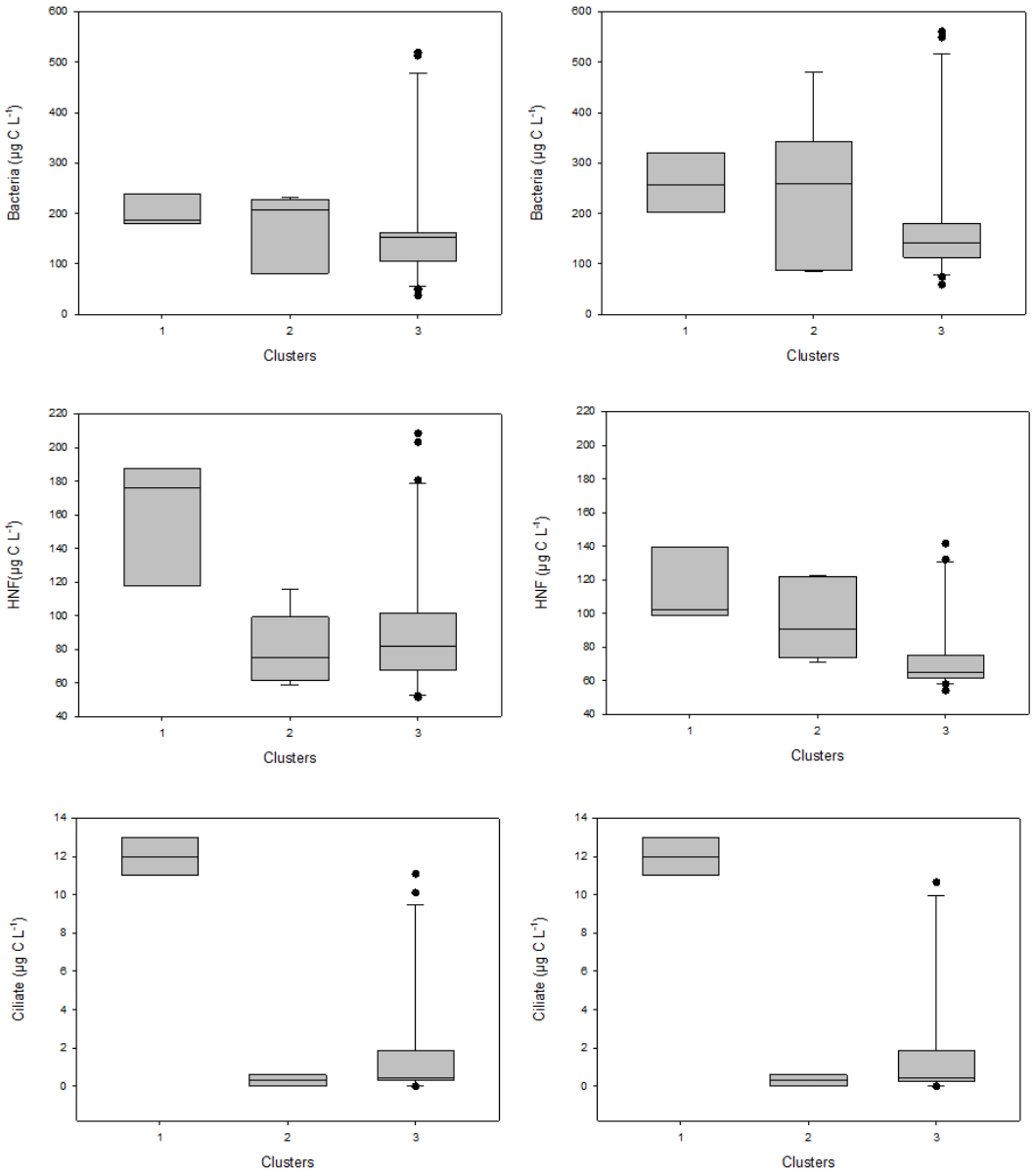


**Figure 3.1-11.** Change in biomasses of bacteria, HNF and ciliate before incubation (left panel) and after incubation (right panel) in clusters of control treatments.

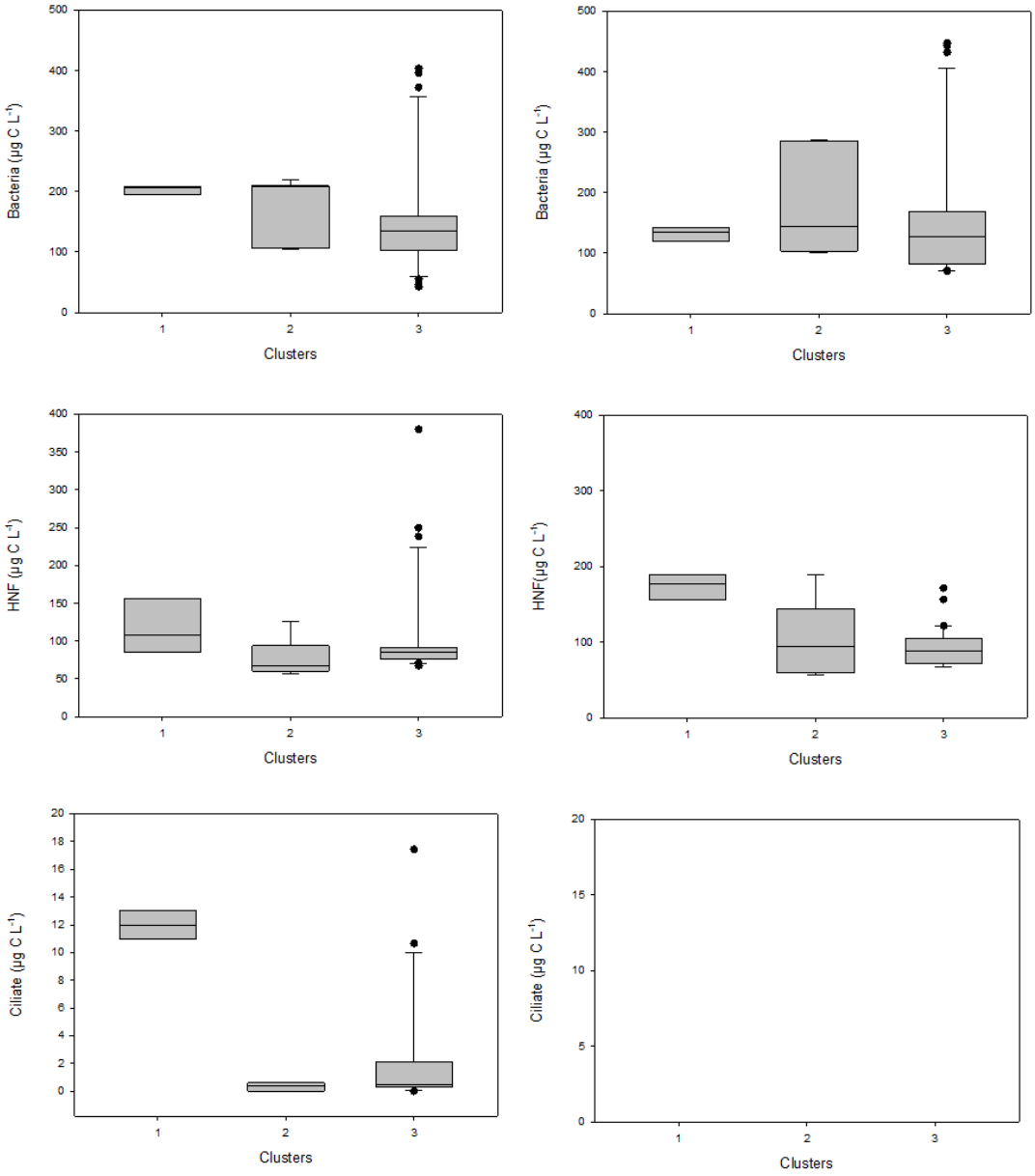


**Figure 3.1-12.** Change in biomasses of bacteria, HNF and ciliate before incubation (left panel) and after incubation (right panel) in clusters of zooplankton treatments.

## 3.2. The relative importance of microbial communities in the planktonic food web of Lakes Eymir and Mogan 2010–2011

### 3.2.1.1 Lake Mogan

### 3.2.1.1 Physical and chemical parameters

RM-one way ANOVA revealed a significant annual difference and the salinity recorded in 2010 was significantly higher than 2011 (Table 3.2.1-1 and Table 3.2.1-2). There was a significant seasonal effect on salinity (Table 3.2.1-1) and winter salinity was higher in both 2010 and 2011 than the other seasons (Figure 3.2.1-1). There were no annual and seasonal differences for water depth (Table 3.2.1-1 and Figure 3.2.1-1).

The pH value was significantly differed between years and it was lower in 2011 than 2010 (Table 3.2.1-1 and Table 3.2.1-2). There was a significant seasonal effect on pH (Table 3.2.1-1) and the pH value was lower in autumn. However; the pH value was significantly higher in autumn 2011 than other seasons.

The annual mean water temperature did not significantly differ between years throughout the study period in Lake Mogan (Table 3.2.1-1). There was a season effect on temperature values (Table 3.2.1-1) and summer temperatures were higher than other seasons in both years.

The mean dissolved oxygen concentration was high and remained so throughout the study period and was not different between years (Table 3.2.1-1). There was a seasonal effect on dissolved oxygen concentrations (Table 3.2.1-1) and it was higher in winter 2010.

Concentrations of total phosphorous (TP) were not significantly different between years (Table 3.2.2-1). There was a seasonal effect on TP concentrations (Table 3.2.1-1) and it was higher in winter 2010 (Figure 3.2.1-2). Concentrations of total nitrogen (TN) were significantly higher in 2010 than in 2011 (Table 3.2.2-1 and Table 3.2.1-2). TN concentrations did not differ between seasons (Figure 3.2.1-3).

**Table 3.2.1-1:** Summary of the univariate repeated measures of one-way ANOVA testing the effect of year and season on some physical and chemical parameters in Lake Mogan. Arrows show the direction of the year effect on the parameters. Significance is indicated as *P < 0.05, **P < 0.01, ***P < 0.001, NS, not significant.

| | **Year** | | **Time (Season)** |
|---|---|---|---|
| **Salinity** | *** | ↓ | * |
| **pH (-log[H+]** | *** | ↓ | *** |
| **Water Temperature (°C)** | NS | | *** |
| **Water Depth (m)** | NS | | NS |
| **Dissolved oxygen mg $L^{-1}$** | NS | | *** |
| **TP µg P $L^{-1}$** | NS | | ** |
| **TN µg N $L^{-1}$** | *** | ↓ | NS |

**Table 3.2.1-2** Annual mean values of physical and chemical parameters of Lake Mogan

| | **2010** | **2011** |
|---|---|---|
| **Salinity $‰$** | 1.72±0.19 | 1.20±0.22 |
| **pH (-log[H+]** | 8.2 0.3 | 7.8±0.5 |
| **Water Temperature (°C)** | 14.0±7.3 | 13.3±7.6 |
| **Water Depth (m)** | 4.1±0.2 | 4.4±0.2 |
| **Dissolved oxygen mg $L^{-1}$** | 8.6± 3 | 7.5 ±1.8 |
| **TP µg P $L^{-1}$** | 81 ±29 | 63 ±11 |
| **TN µg N $L^{-1}$** | 1643 ±351 | 575 ±215 |

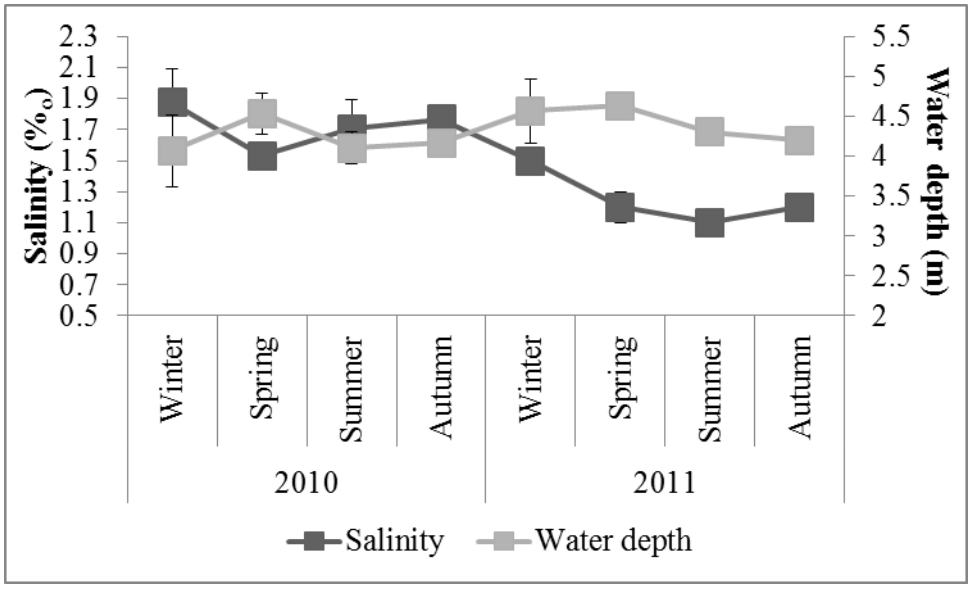


**Figure 3.2.1-1.** Seasonal change in salinity and water depth between 2010 and 2011 in Lake Mogan.

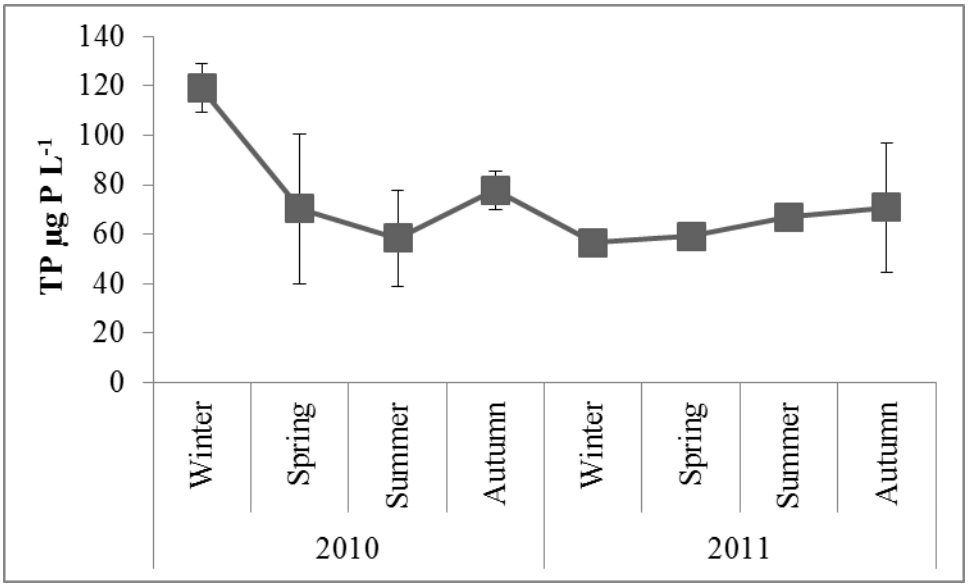


**Figure 3.2.1-2.** Seasonal change in TP concentrations between 2010 and 2011 in Lake Mogan.

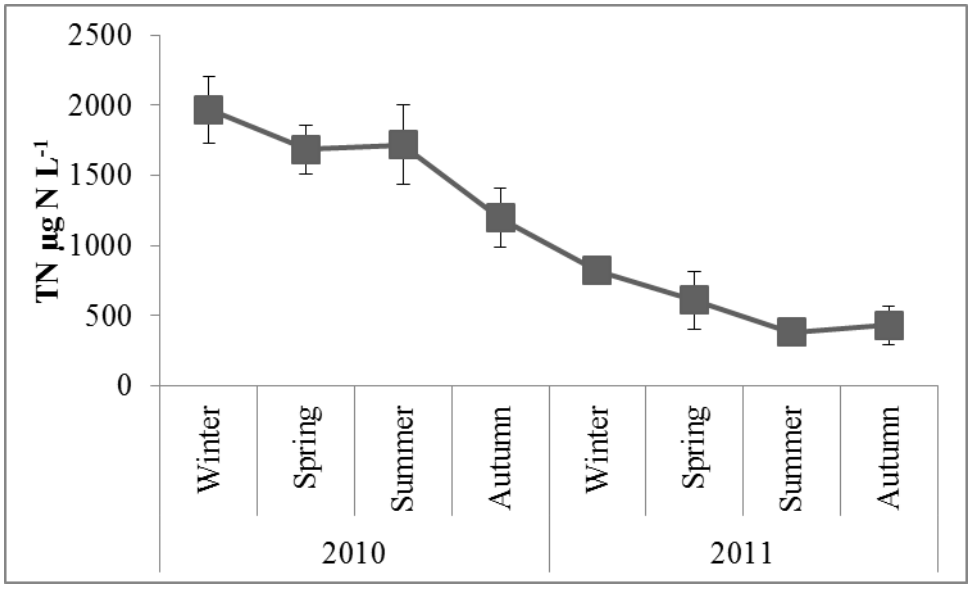


**Figure 3.2.1-3** Seasonal change in TN concentrations between 2010 and 2011 in Lake Mogan.

### 3.2.1.2. Biological parameters

**Bacteria:** RM-ANOVA results showed significant year and habitat interactions effect for bacteria biomass (Table 3.2.1-3). There was lower bacteria biomass in the littoral habitat in 2011 (Table 3.2.1-4). RM-ANOVA showed seasonal effect (Table 3.2.1-3) for bacteria biomass. Autumn bacterial biomass was lower in autumn 2010 in both pelagic and littoral habitats (Figure 3.2.1-4a). Winter bacterial biomass was higher in both pelagic and littoral habitats than the other seasons in 2011 (Figure 3.2.1-4a).

**Table 3.2.1-3:** Summary of the univariate repeated measures of two-way ANOVA testing the effect of year, habitat and seasons on biomass of microbes and other plankton in Lake Mogan. Arrows show the direction of the year and habitat effect on the organisms and ratios.
Significance is indicated as *P < 0.05, **P < 0.01, ***P < 0.001, NS, not significant.

| | Year (Y) | | Habitat (H) | | Y X H | | Season |
|---|---|---|---|---|---|---|---|
| **Bacteria** | ** | | ** | | * | ↓ | *** |
| **HNF** | NS | | NS | | NS | | *** |
| **Ciliate** | *** | ↓ | NS | | NS | | NS |
| **T.zooplankton** | ** | ↑ | NS | | NS | | NS |
| **Cladocera** | * | ↑ | NS | | NS | | NS |
| **Copepoda** | NS | | NS | | NS | | *** |
| **Rotifera** | *** | | *** | | *** | ↑ | * |
| **HNF:Bacteria** | *** | | ** | | ** | ↑ | * |
| **Ciliate:HNF** | ** | ↓ | NS | | NS | | NS |
| **Copepoda:Bacteria** | ** | ↑ | NS | | NS | | ** |
| **Copepoda:HNF** | * | ↑ | NS | | NS | | ** |
| **Copepoda:Ciliate** | NS | | NS | | NS | | NS |
| **Cladocera:Bacteria** | ** | ↑ | NS | | NS | | NS |
| **Cladocera:HNF** | * | ↑ | NS | | NS | | NS |
| **Cladocera:Ciliate** | * | ↑ | NS | | NS | | NS |
| **Rotifera:Bacteria** | *** | ↑ | NS | | NS | | *** |
| **Rotifera:HNF** | *** | ↑ | NS | | NS | | *** |
| **Rotifera:Ciliate** | * | ↑ | NS | | NS | | *** |
| **Zooplankton:Bacteria** | ** | ↑ | * | ↓ | NS | | NS |
| **Zooplankton:HNF** | * | ↑ | NS | | NS | | NS |
| **Zooplankton:Ciliate** | NS | | NS | | NS | | NS |

**Table 3.2.1-4** Annual mean values of biological parameters in the pelagic and littoral zones of Lake Mogan

| | **2010** | | **2011** | |
|---|---|---|---|---|
| **Biomass (µg C $L^{-1}$)** | **Pelagic** | **Littoral** | **Pelagic** | **Littoral** |
| Bacteria | 194±62 | 123±46 | 122±73 | 112±56 |
| HNF | 103±28 | 111±40 | 107±38 | 98±31 |
| Ciliate | 1.6±1.3 | 2.5±2.2 | 0.2±0.1 | 0.5±0.2 |
| Phytoplankton | 621±459 | | 147±122 | |
| T.Zooplankton | 23±20 | 2±1 | 51±30 | 56±46 |
| Cladocera | 4±3 | 0.3±0.2 | 42±30 | 38±29 |
| Copepoda | 17±10 | 2±1 | 7±6 | 9±5 |
| Rotifera | 1.4±1 | 0.1±0.1 | 2±1 | 9±6 |

**HNF:** RM-ANOVA results showed that there were no annual and habitat differences for the HNF biomass (Table 3.2.1-3). There was a significant seasonal difference for the HNF biomass (Table 3.2.1-3). HNF biomass was higher in autumn 2010 and lower in winter 2011 than the other seasons in both pelagic and littoral zones of the lake (Figure 3.2.1-4b).

There were annual and habitat differences for the HNF: bacteria ratio (Table 3.2.1-3). In the pelagic zone, HNF: bacteria ratio was higher in 2011 than in 2010. Habitat difference was only observed in 2010 and HNF: bacteria ratio was higher in the littoral zone than the pelagic zone.

RM-ANOVA results also showed a seasonal effect for the HNF: bacteria ratio (Table 3.2.1-3) and it was higher in autumn 2010 and lower in winter 2011 than the other seasons in both pelagic and littoral zones of the lake.

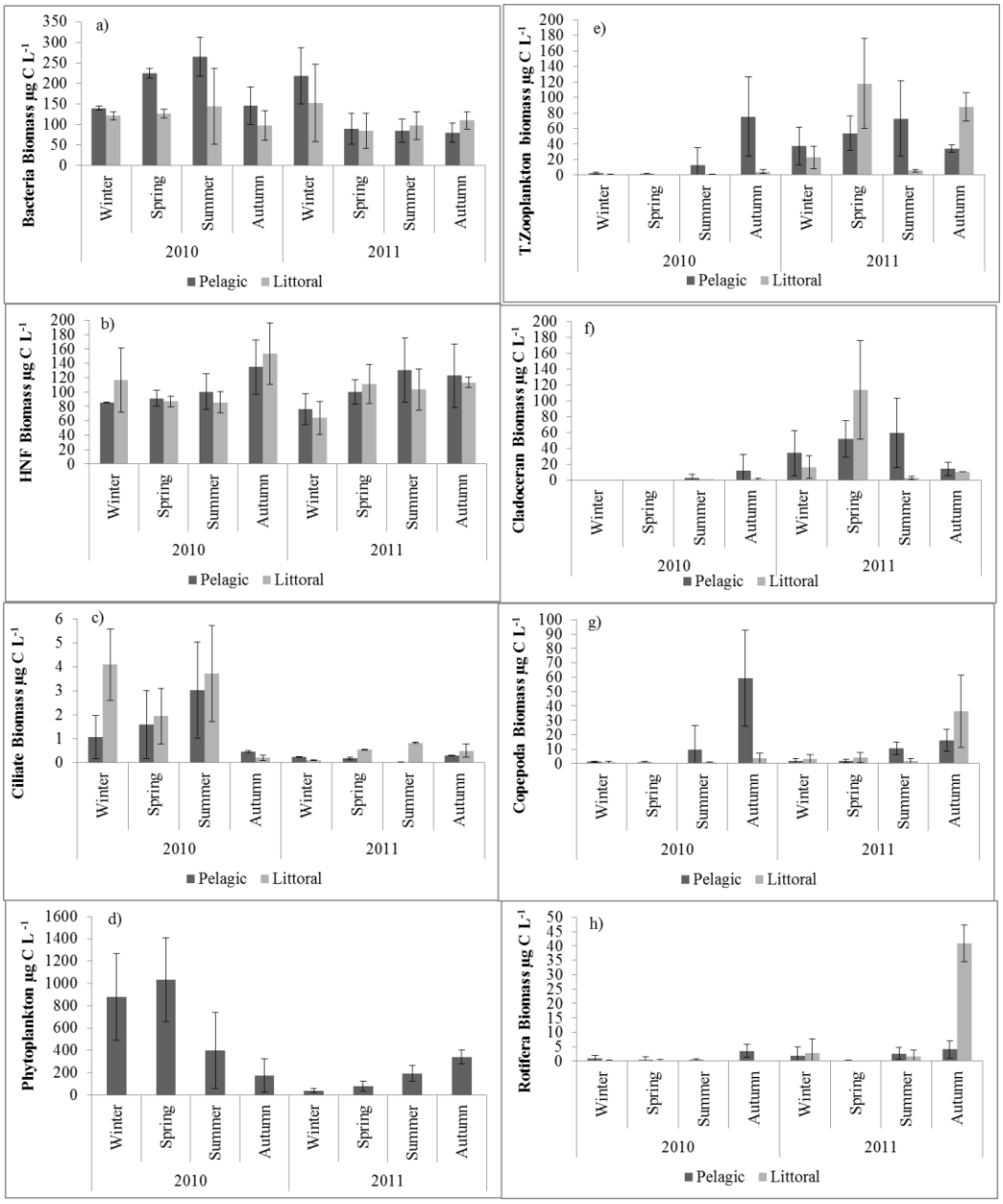


**Figure 3.2.1-4** Seasonal biomasses (± 1 SD) of (a) bacteria, (b) HNF, (c) ciliates, (d) phytoplankton, (e) total zooplankton, (f) Cladocera, (g) Copepoda, and (h) Rotifera in pelagic and littoral zones of Lake Mogan between 2010 and 2011.

**Ciliate**: Oligotrichida dominated in both 2010 and 2011 and included the genera *Strobilidium, Strombidium, Pelagostrombidium* and *Halteria* in both pelagic and littoral zones of the lake.

RM-ANOVA results revealed that there was annual difference for ciliate biomass (Table 3.2.1-3). Ciliate biomass was lower in 2011 than in 2010 in both pelagic and littoral habitats (Table 3.2.1-4). There were no habitat and seasonal differences for ciliate biomass (Table 3.2.1-3).

There was an annual difference for the ciliate: HNF ratios (Table 3.2.1-3) and it was lower in 2011 than in 2010 in both pelagic and littoral zones of the lake .

**Phytoplankton**: RM-ANOVA showed an annual difference for the phytoplankton biomass of Lake Mogan (p: 0.01) and it ranged between 91 and 1401 μg C $L^{-1}$ in 2010 (Figure 3.2.1-4d). Phytoplankton biomass ranged between 22 and 385 μg C $L^{-1}$ in 2011 that was lower than in 2010 (Figure 3.2.1-4d). There was also seasonal effect on the phytoplankton biomass (p: 0.001) and it was lower in autumn 2010 and winter 2011 (Figure 3.2.1-4d).

Bacteria: phytoplankton ratio was significantly different between years (p: 0.02) and higher in 2011 than 2010. There was a seasonal effect on bacteria: phytoplankton ratio (p: 0.02) and it was lower in winter 2010 and higher in winter 2011 than the other seasons.

**Zooplankton**: There was significant difference for the zooplankton biomass between years (Table 3.2.1-3). There were higher total zooplankton biomasses in 2011 than in 2010 in both pelagic and littoral habitats (Table 3.2.1-4).

There were annual differences for zooplankton: bacteria and zooplankton: HNF ratios (Table 3.2.1-3). Zooplankton: bacteria and zooplankton: HNF ratios were

significantly higher in 2011 than in 2010 in both pelagic and littoral zones of lake.

There was difference between habitats for zooplankton: bacteria ratio (Table 3.2.1-3) and it was higher in the pelagic zone of the lake. There were no annual, seasonal and habitat differences for the zooplankton: ciliate ratio.

**Cladocera:** In both pelagic and littoral zone of the lake, *Diaphanosoma lacustris* (Korinek) was the most abundant species in 2010. *Chydorus sphaericus* (O.F. Müller) and *D. lacustris* were the most abundant species in 2011.

RM-ANOVA results revealed that there was significant difference for the cladoceran biomass between years (Table 3.2.1-3). Cladocera biomass was significantly higher in 2011 than in 2010 in both pelagic and littoral habitats (Table 3.2.1-4).

There were annual differences for the cladocera: bacteria cladocera: HNF and cladocera: ciliate ratios (Table 3.2.1-3) and they were higher in 2011 in both pelagic and littoral zones. Cladoceran: phytoplankton ratio significantly differed between years (p: 0.01) and it was higher in 2011.

**Copepoda:** *Arctodiaptomus bacillifer* (Koelbel) was the most abundant species in both 2010 and 2011 in both pelagic and littoral zones of the lake.

There were no annual and habitat differences for the copepod biomass (Table 3.2.1-3). There was a statistically significant seasonal effect for the copepod biomass (Table 3.2.1-3). In the pelagic zone, autumn copepod biomass was higher than other seasons in 2010 (Figure 3.2.1-4g). However, autumn copepod biomass was higher than other seasons in 2011 in the littoral zone (Figure 3.2.1-4g).

There were significant annual differences for the copepod: bacteria and copepod: HNF ratios (Table 3.2.1-3) and they were higher in 2011. There were also significant

seasonal effect for the copepod: bacteria and copepod:HNF ratios (Table 3.2.1-3) and they were higher in autumn in both 2010 and 2011.

**Rotifera:** In both habitat, *Brachionus sp.* and *Keratella quadrata* (Müller) were the most abundant species in 2010 and *K. quadrata*, *Asplanchna sp.* and *Hexarthra mira* (Hudson) were the most abundant species in 2011.

There were annual and habitat interaction effect for rotifer biomass (Table 3.2.1-3). There was less total rotifer biomass in the littoral zone than the pelagic zone in 2010 (Table 3.2.1-4). In contrast to this, there was higher total rotifer biomass in 2011 in the littoral zone of the lake (Table 3.2.1-4). There was a seasonal difference for total rotifer biomass in 2010 in the littoral zone (Table 3.2.1-3) and there was higher total rotifer biomass in autumn 2011 (Figure 3.2.1-4).

Rotifer: bacteria, rotifer: HNF androtifer: ciliate ratios were significantly differed between years (Table 3.2.1-3) and they were higher in 2011. There were seasonal effect for rotifer: bacteria, rotifer:HNF and rotifer:ciliate ratios (Table 3.2.1-3) and they were higher in autumn 2011 than the other seasons.

**Aquatic Plants:**

In Lake Mogan, the average PVI % of lake was 13.8 % during the plant survey carried out in summer 2010, *P. pectinatus,* and *Najas spp.* were recorded as dominant submerged plant species. In the plant survey carried out in 2011, the average PVI% of lake was lower than 2011 (PVI 1.4 %). The same species were observed.

**Fish:**

In 2010, the fish biomass of Lake Mogan was 1.7 CPUE kg $net^{-1}$ in the pelagic zone of the lake and 1 CPUE kg $net^{-1}$ in the littoral zone of the lake. *Tinca tinca*

*(*Linnaeus, 1758), *Cyprinus carpio* (Linnaeus, 1758) and *Pseudorasbora parva* (Temmnick & Schlegel, 1846) were the observed species in both pelagic and littoral zone of the lake.

In 2011, the fish biomass was 1.06 CPUE kg net$^{-1}$ in the pelagic zone of the lake and 0.63 CPUE kg net$^{-1}$ in the littoral zone of the lake. The same species were observed.

### 3.2.1.3 Proportion of zooplankton, phytoplankton and microbial biomass.

The estimated contribution of phytoplankton to total plankton biomass was significantly lower in 2011 than 2010 (p: 0.02), (Figure 3.2.1-5). There was a seasonal effect on the estimated contribution of phytoplankton to total plankton biomass (p: 0.009) and it was higher in all seasons except autumn in 2010, while the opposite trend was observed in 2011, (Figure 3.2.1-5).

The estimated contribution of total microbial biomass to total plankton biomass was significantly higher in 2011 than in 2010 (p: 0.03), (Figure 3.2.1-5). There was a seasonal effect on the estimated contribution of total microbial biomass to total plankton biomass (p: 0.02) and it was higher in summer and autumn 2010 and winter 2011 (Figure 3.2.1-5).

The contribution of zooplankton to total plankton biomass was significantly higher in 2011 than in 2010 (p: 0.01), (Figure 3.2.1-5). There were no seasonal differences for the contribution of zooplankton in both years.

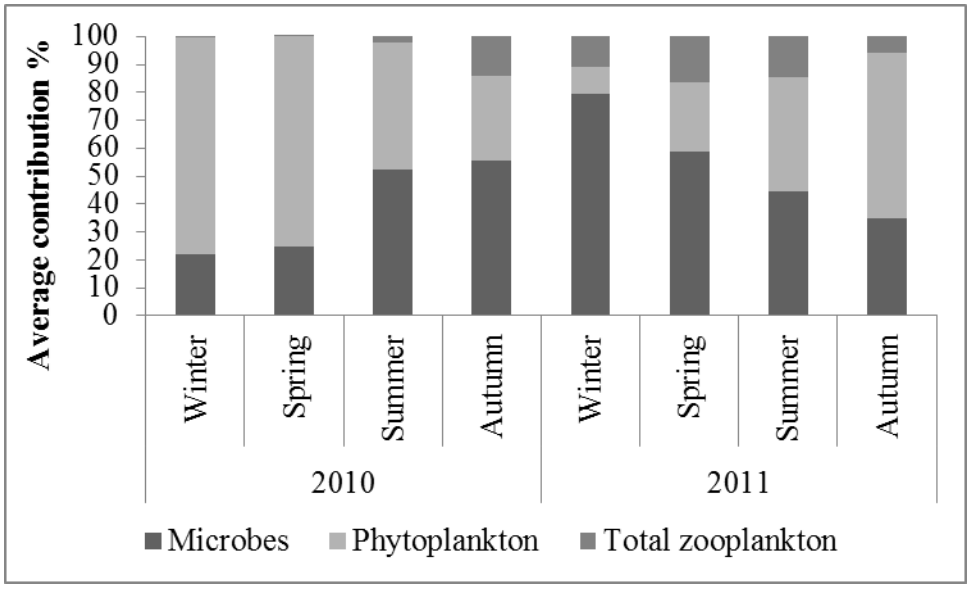


**Figure 3.2.1-5.** Seasonal average contribution (%) of zooplankton, phytoplankton and microbes (the sum of HNF, ciliates and bacterioplankton) to total plankton biomass in pelagic zone of Lake Mogan between 2010 and 2011.

### 3.2.2 Lake Eymir

#### 3.2.2.1 Physical and chemical parameters

RM one way ANOVA revealed a significant annual difference and the salinity recorded in 2010 was higher than 2011 (Table 3.2.2-1 and Table 3.2.2-2). There was a seasonal effect for salinity (Table 3.2.2-1) and winter salinity in 2010 was higher than the other seasons (Figure 3.2.2-1). Water depth significantly differed between years (Table 3.2.2-1) and it was higher in 2011 than in 2010 (Table 3.2.2-2 and Figure 3.2.2-1). There was a seasonal effect for water depth (Table 3.2.2-1) and winter water depth in 2010 was significantly lower than the other seasons (Figure 3.2.2-1).

In Lake Eymir, there were no differences for the pH values between years (Table 3.2.2-1). There was a seasonal effect for pH (Table 3.2.2-1) and the winter pH was significantly lower than the other seasons in 2011.
The annual mean water temperature did not significantly differ between years throughout the study period in Lake Eymir (Table 3.2.2-1). There was a seasonal effect for temperature (Table 3.2.2-1) and summer temperatures were higher than other seasons in both years.

The mean dissolved oxygen concentration was high and remained so throughout the study period in Lake Eymir in both lakes (Table 3.2.2-1). There was a seasonal effect for dissolved oxygen (Table 3.2.2-1) and it was higher in winter 2010.

In Lake Eymir, the concentrations of total phosphorous (TP) significantly differed between years (Table 3.2.2-1) and it was higher in 2010 than 2011 (Table 3.2.2-2). There was a significant seasonal effect on TP concentrations (Table 3.2.2-1) and it was higher in autumn 2010 than the other seasons in 2010 (Figure 3.2.2-2). There was a annual difference for the TN concentration of Lake Eymir (Table 3.2.2-1) and it was higher in 2010 (Table 3.2.2-2 and Figure 3.2.2-3).

**Table 3.2.2-1: Summary of the univariate repeated measures of one-way ANOVA testing the effect of year and season on some physical and chemical parameters in Lake Eymir. Arrows show the direction of the year effect on the parameters. Significance is indicated as *P < 0.05, **P < 0.01, ***P < 0.001, NS, not significant.**

| | Year | | Time (Season) |
|---|---|---|---|
| **Salinity** | *** | ↓ | * |
| **pH (-log[H+]** | NS | | ** |
| **Water Temperature (°C)** | NS | | ** |
| **Water Depth (m)** | * | ↑ | * |
| **Dissolved oxygen mg $L^{-1}$** | NS | | *** |
| **TP µg P $L^{-1}$** | ** | ↓ | ** |
| **TN µg N $L^{-1}$** | *** | ↓ | NS |

**Table 3.2.2-2 Annual mean values of physical and chemical parameters of Lake Eymir**

| | Lake Eymir | |
|---|---|---|
| | **2010** | **2011** |
| **Salinity $‰_0$** | 1.44±0.14 | 1.20±0.19 |
| **pH (-log[H+]** | 8.0±0.3 | 7.8± 0.6 |
| **Water Temperature (°C)** | 13.5±7.8 | 13.5±7.8 |
| **Water Depth** | 5.4±0.5 | 5.8±0.2 |
| **Oxygen mg $L^{-1}$** | 6.1±2.4 | 6.1±2.4 |
| **TP µg P $L^{-1}$** | 198± 60 | 95 ±33 |
| **TN µg N $L^{-1}$** | 2041± 277 | 594 ±188 |

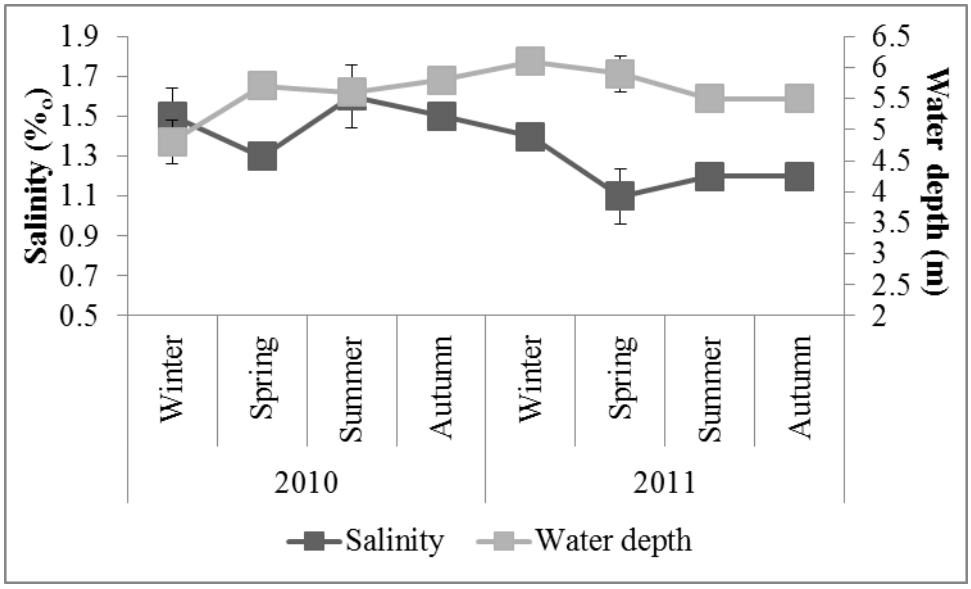


**Figure 3.2.1-1** Seasonal change in salinity and water depth between 2010 and 2011 in Lake Eymir.

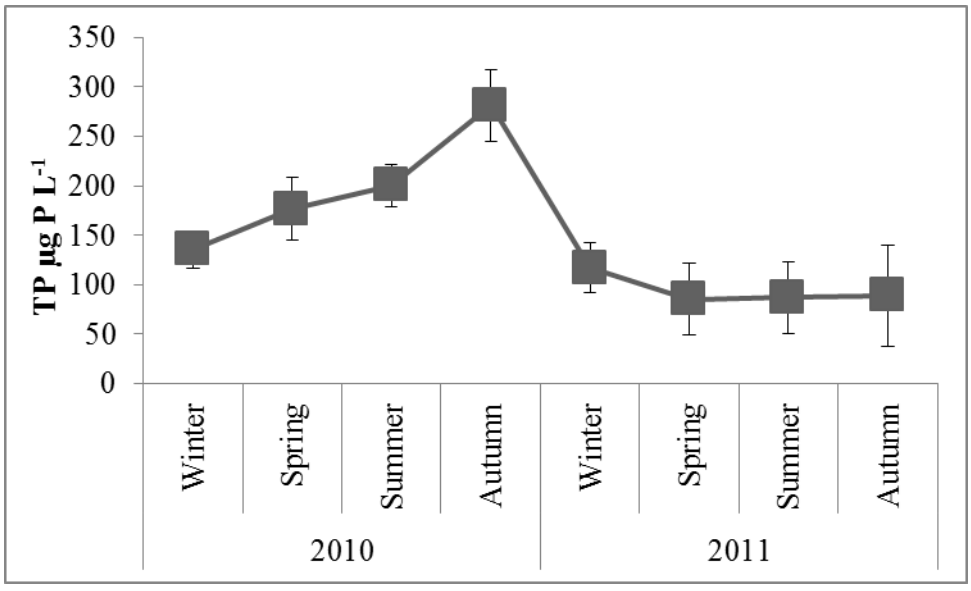


**Figure 3.2.2-2** Seasonal change in TP concentrations between 2010 and 2011 in Lake Eymir.

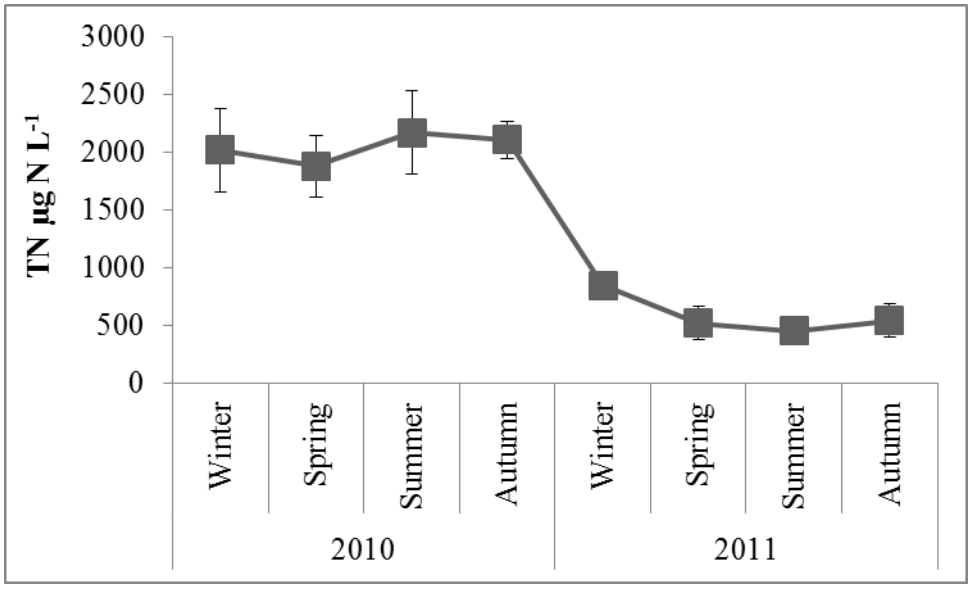


**Figure 3.2.2-3** Seasonal change in TN concentrations between 2010 and 2011 in Lake Eymir.

### 3.2.2. Biological parameters

**Bacteria**: There was no statistically significant annual difference for bacteria biomass. However there was a significant habitat difference for bacteria biomass (Table 3.2.2-3). In the pelagic zone, bacteria biomass ranged between 44 and 150 µg C $L^{-1}$ in 2010 and ranged between 24 and 160 µg C $L^{-1}$ in 2011 (Figure 3.2.2-4a), (Table 3.2.2-4). There was significantly less bacteria biomass in the littoral habitat than the pelagic habitat in both years. In littoral habitat, bacteria biomass ranged between 29 and 96 µg C $L^{-1}$ in 2010 and ranged between 28 and 140 µg C $L^{-1}$ in 2011 (Table 3.2.2-4), (Figure 3.2.2-4a). There was a significant seasonal effect for bacteria biomass (Table 3.2.2-3). Winter bacterial biomass was higher than the other seasons in 2011 (Figure 3.2.2-4a)

**HNF**: There was a significant annual difference for the HNF biomass (Table 3.2.2-3). There was higher HNF biomass in 2011 than in 2010 in both pelagic and littoral habitats (Figure 3.2.2-4b and Table 3.2.2-4). There was a statistically significant seasonal effect for HNF biomass (Table 3.2.2-3) Autumn HNF biomass was higher than the other seasons in 2011 in both pelagic and littoral zones (Figure 3.2.2-4b).
There were statistically significant annual and seasonal differences for the HNF: bacteria ratios which were higher in 2011, especially in autumn 2011 in both pelagic and littoral habitats of the lake (Table 3.2.2-4).

**Ciliate:** Oligotrichida dominated in both pelagic and littoral zones and in both 2010 and 2011 and included the genera *Strobilidium, Strombidium,* and *Halteria*. There were no statistically significant annual, seasonal and habitat differences for the ciliate biomass (Table 3.2.2-3).

There were no statistically significant annual, seasonal or habitat differences for the ciliate: HNF ratios (Table 3.2.2-3)

**Phytoplankton:** RM-one way ANOVA revealed significant annual difference for phytoplankton biomass (p: 0.01) and it ranged between 27 and 2387 µg C $L^{-1}$ in 2010 (Figure 3.2.2-4d) and 81 and 1390 µg C $L^{-1}$ in 2011.There was no significant seasonal effect for phytoplankton biomass in Lake Eymir.

There were no statistically significant annual and seasonal differences for the bacteria: phytoplankton ratio.

**Table 3.2.2-3:** Summary of the univariate repeated measures of two-way ANOVA testing the effect of year, habitat and season on biomass of microbes and other plankton in Lake Eymir. Arrows show the direction of the year and habitat effect on the organisms and ratios.
Significance is indicated as *P < 0.05, **P < 0.01, ***P < 0.001, NS, not significant.

| | Year (Y) | | Habitat (H) | | Y X H | Season |
|---|---|---|---|---|---|---|
| **Bacteria** | NS | | * | ↓ | NS | *** |
| **HNF** | ** | ↑ | NS | | NS | *** |
| **Ciliate** | NS | | NS | | NS | NS |
| **T.zooplankton** | NS | | NS | | NS | NS |
| **Cladocera** | NS | | NS | | NS | NS |
| **Copepoda** | NS | | NS | | NS | * |
| **Rotifera** | * | ↓ | NS | | NS | NS |
| **HNF:Bacteria** | ** | ↑ | NS | | NS | ** |
| **Ciliate:HNF** | NS | | NS | | NS | NS |
| **Copepoda:Bacteria** | NS | | NS | | NS | NS |
| **Copepoda:HNF** | * | ↓ | NS | | NS | ** |
| **Copepoda:Ciliate** | NS | | NS | | NS | NS |
| **Cladocera:Bacteria** | NS | | NS | | NS | NS |
| **Cladocera:HNF** | NS | | NS | | NS | NS |
| **Cladocera:Ciliate** | NS | | NS | | NS | NS |
| **Rotifera:Bacteria** | NS | | NS | | NS | NS |
| **Rotifera:HNF** | NS | | NS | | NS | NS |
| **Rotifera:Ciliate** | * | ↓ | NS | | NS | NS |
| **Zooplankton:Bacteria** | NS | | NS | | NS | NS |
| **Zooplankton:HNF** | NS | | NS | | NS | NS |
| **Zooplankton:Ciliate** | NS | | NS | | NS | NS |

**Table 3.2.2-4 Annual mean values of biological parameters in the pelagic and littoral zones of Lake Eymir**

| | 2010 | | 2011 | |
|---|---|---|---|---|
| | **Pelagic** | **Littoral** | **Pelagic** | **Littoral** |
| Bacteria | 89±30 | 62±25 | 79±48 | 70±35 |
| HNF | 71±12 | 80±35 | 127±103 | 92±63 |
| Ciliate | 3.7±3 | 3.7±3 | 2.1±2 | 1.8±1 |
| Phytoplankton | 1114±915 | | 446±406 | |
| T.Zooplankton | 72±70 | 54±50 | 36±30 | 44±40 |
| Cladocera | 27±20 | 7±5 | 24±20 | 28±20 |
| Copepoda | 17±10 | 14±10 | 7±5 | 10±8 |
| Rotifera | 29±20 | 35±30 | 6±5 | 7±5 |

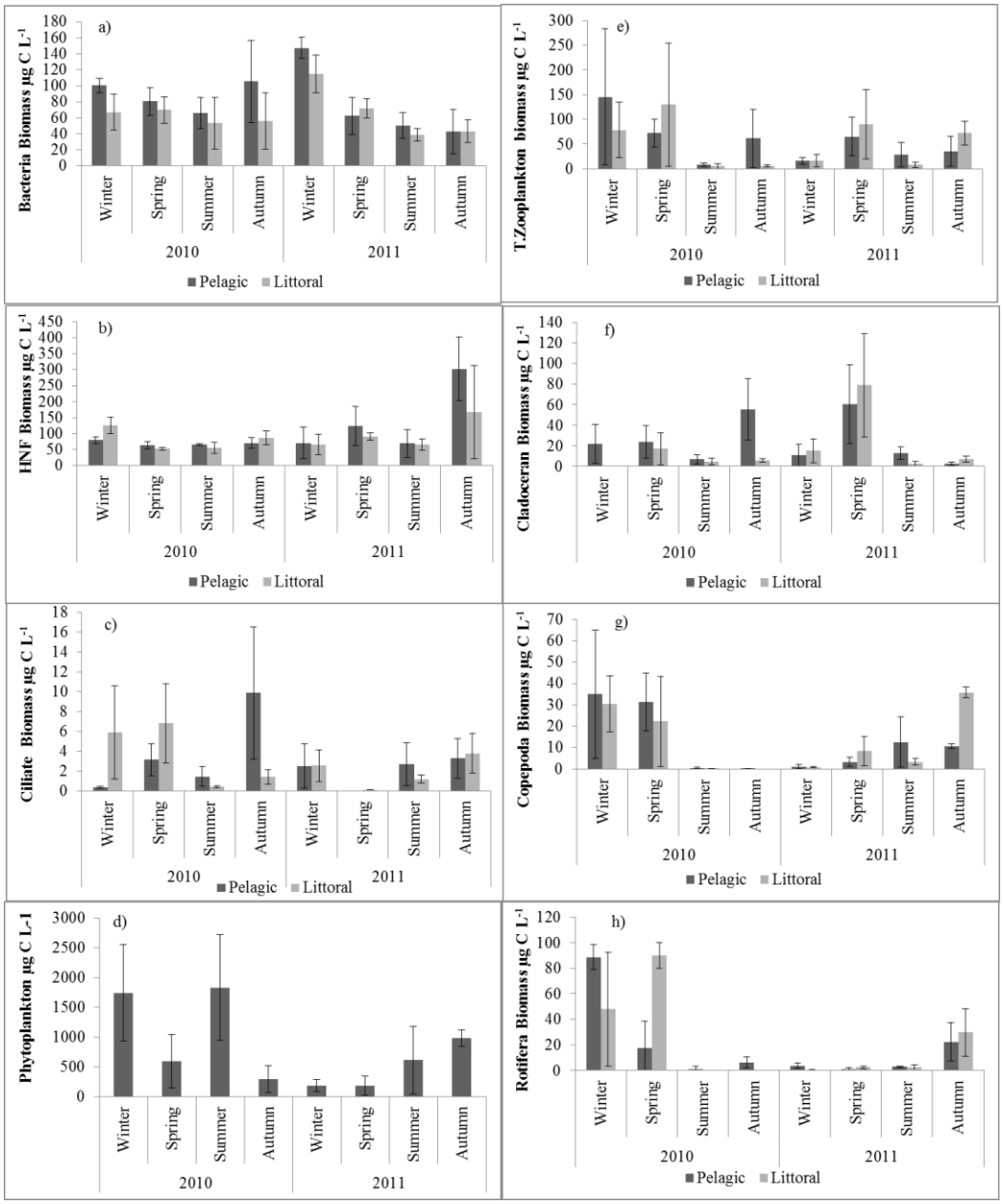


**Figure 3.2.2-.4** Seasonal biomasses (± 1 SD) of (a) bacteria, (b) HNF, (c) ciliates, (d) phytoplankton, (e) total zooplankton, (f) Cladocera, (g) Copepoda, and (h) Rotifera in pelagic and littoral zones of Lake Eymir between 2010 and 2011.

**Zooplankton:** There were no statistically significant annual, habitat and seasonal differences for the total zooplankton biomass in Lake Eymir (Table 3.2.2-3).
There were no statistically significant annual, habitat and seasonal differences for the zooplankton: bacteria, zooplankton: HNF, zooplankton: ciliate and zooplankton: phytoplankton ratios (Table 3.2.2-3).

**Cladocera:** *Daphnia pulex* (de Geer) and *D lacustris* were the most abundant species in 2010. *Daphnia magna* (Straus) was the most abundant species in 2011.
There were no statistically significant annual, habitat and seasonal differences for cladoceran biomass.

There were no statistically significant differences for the cladoceran: HNF and cladocera: ciliate ratios between years, habitats and seasons.

**Copepoda:** *A. bacillifer* was the most abundant species in both pelagic and littoral zones and in both 2010 and 2011.

There were no statistically significant annual or habitat differences for the copepoda biomasses. There was a statistically significant seasonal difference for the copepod biomass (Table 3.2.2-3). Copepod biomasses were higher in winter 2010 and lower in winter 2011 than the other seasons (Figure 3.2.2-4g).

There were no statistically significant annual, habitat and seasonal differences for the copepod: bacteria and copepod: ciliate ratios. Copepod: HNF ratios were significantly differed between seasons (Table 3.2.2-3) and it was higher in spring and winter than the other seasons in 2010.

**Rotifera:** In the pelagic habitat, *Rotaria sp.* and *Polyarthra sp.* were the most abundant species in 2010. *Keratella quadrata* (Müller) and *Filinia longiseta* (Ehrenberg) were the most abundant species in 2011. In littoral habitat, *K.*

*quadrata* and *Brachionus sp* were the most abundant species in both 2010 and 2011. There was a statistically significant annual difference for the rotifer biomass (Table 3.2.2-3). Rotifer biomass was higher in 2010 than in 2011 in both pelagic and littoral habitats of the lake (Table 3.2.2-4 and Figure 3.2.2-4h).

There were no statistically significant annual, seasonal and habitat differences for the rotifer: bacteria and rotifer: HNF ratios. Rotifer: ciliate ratio significantly differed between years (Table 3.2.2-3) and higher in 2010.

**Aquatic Plants**

In the plant survey carried out in 2010, the average PVI % of Lake Eymir was about 4 %. *P. pectinatus*, and *Najas marina* were recorded as submerged plant species. In the plant survey carried out in 2011, there was no submerged plant recorded in Lake Eymir.

**Fish**

In 2010, the fish biomass of Lake Eymir was 0.5 CPUE kg net$^{-1}$ in the littoral zone of the lake and there was no fish caught in the pelagic zone. *Tinca. tinca* (Linnaeus, 1758), and *Pseudorasbora parva* (Temmnick & Schlegel, 1846) were the observed species in the littoral zone of the lake. In 2011, the fish biomass was 2.2 CPUE kg net$^{-1}$ in the littoral zone of the lake and there was no fish in the pelagic zone. *T. tinca, Cyprinus carpio* (Linnaeus, 1758), and *P. parva* were the observed species in the littoral zone of the lake.

### 3.2.2.3 Proportion of zooplankton, phytoplankton and microbial biomass.

The estimated contribution of phytoplankton to total plankton biomass did not differed between years and among seasons. (Figure 3.2.2-5). The contributions of microbial community were significantly differed between years (p:0.02) and higher in 2011 than in 2010 (Figure 3.2.2-5).

There was no difference between years and among seasons for the contribution of zooplankton (Figure 3.2.2-5).

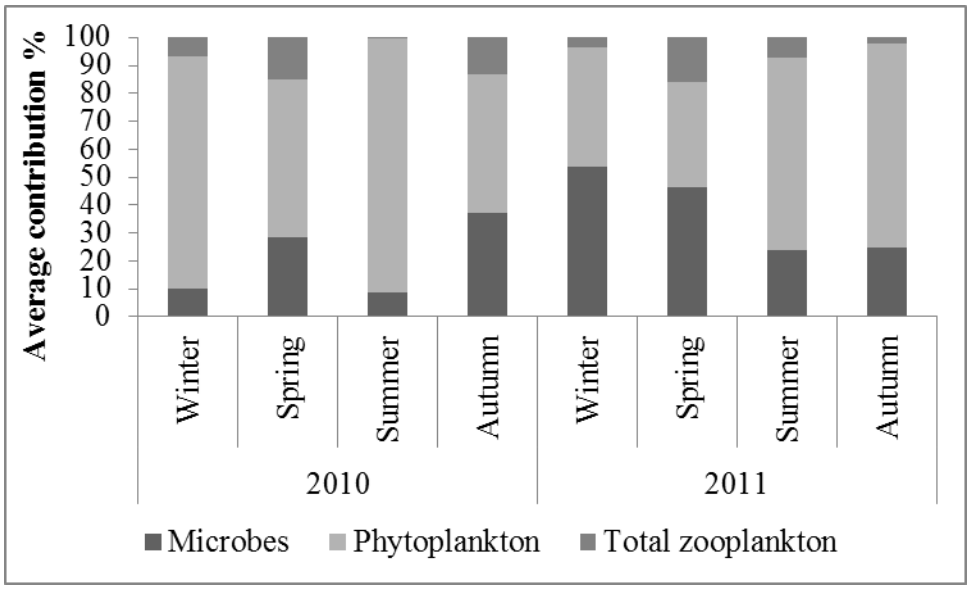


**Figure 3.2.2-5.** Seasonal average contribution (%) of zooplankton, phytoplankton and microbes (the sum of HNF, ciliates and bacterioplankton) to total plankton biomass in pelagic zone of Lake Eymir.

## 3.3 Eymir mesocosm experiment

### 3.3.1 Water level

During the experiment the water level declined in all mesocosms. Water depths in the shallow and deep mesocosms (LW and HW) ranged between 0.8-1 m and 1.6-1.7 m, respectively, at the beginning of the experiment followed by a 0.41 ± 0.06 m decrease in both types of mesocosms (Figure 3.3.1).

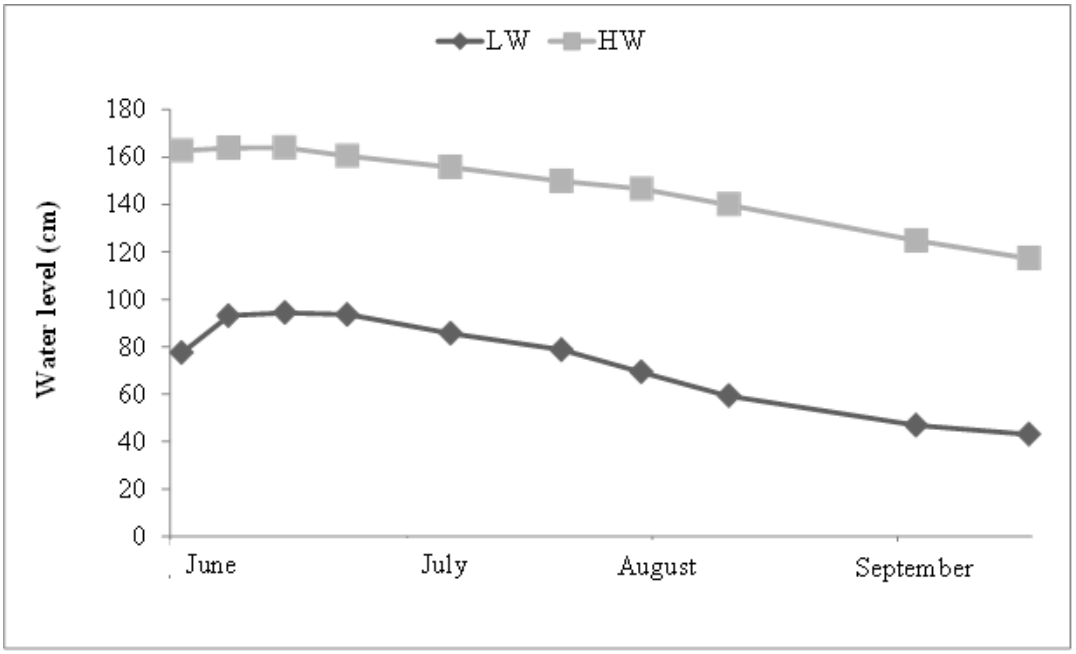


**Figure 3.3.1** Changes in mean water level throughout the experiment.

### 3.3.2 Nutrients

Both water level and fish treatment had a significant effect on TP concentrations (Table 3.3.1). A reduced water level and the presence of fish triggered an increase in TP concentrations as evidenced by the pronounced increase in TP especially in HW+ mesocosms in July (Figure 3.3.2). At the termination of the experiment LW- differed from HW-, being lower in the latter Figure 3.3.2).

Both water level and fish treatment had a significant effect on TN concentrations (Table 3.3.1). With declining water levels, TN concentrations increased in August and onwards. LW mesocosms overall had higher TN concentrations than HW (Figure 3.3.3). Fishless mesocosms had lower TN concentrations than LW+ and HW+ mesocosms in August and September. (Table 3.3.1, Figure 3.3.3).

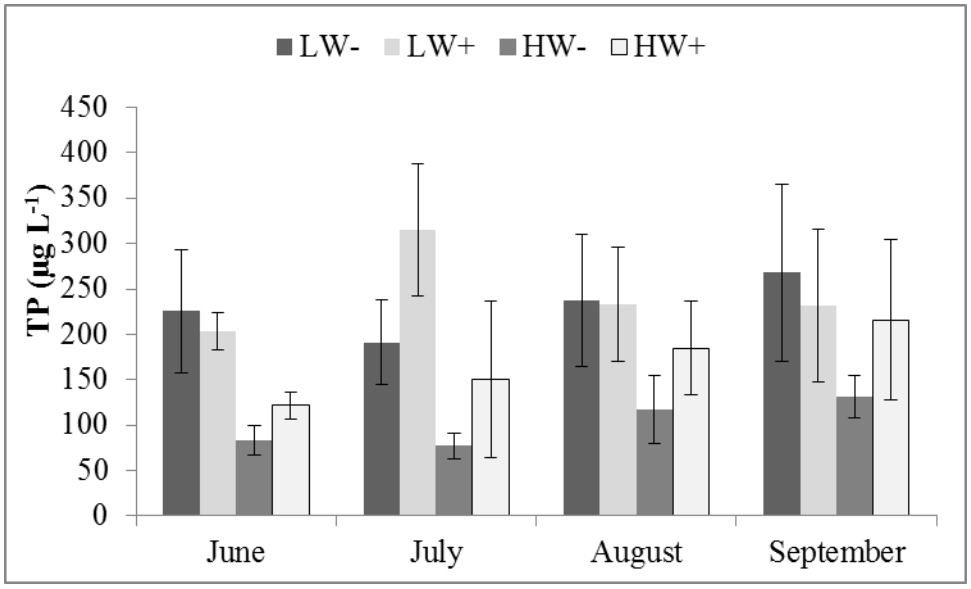


**Figure 3.3.2** Monthly mean concentrations (± 1 SD) of total phosphorus (TP) in Low water fishless (LW-), Low water with fish (LW+), High water fishless (HW-) and High water with fish (HW+) mesocosms (data taken from Bucak (2011).

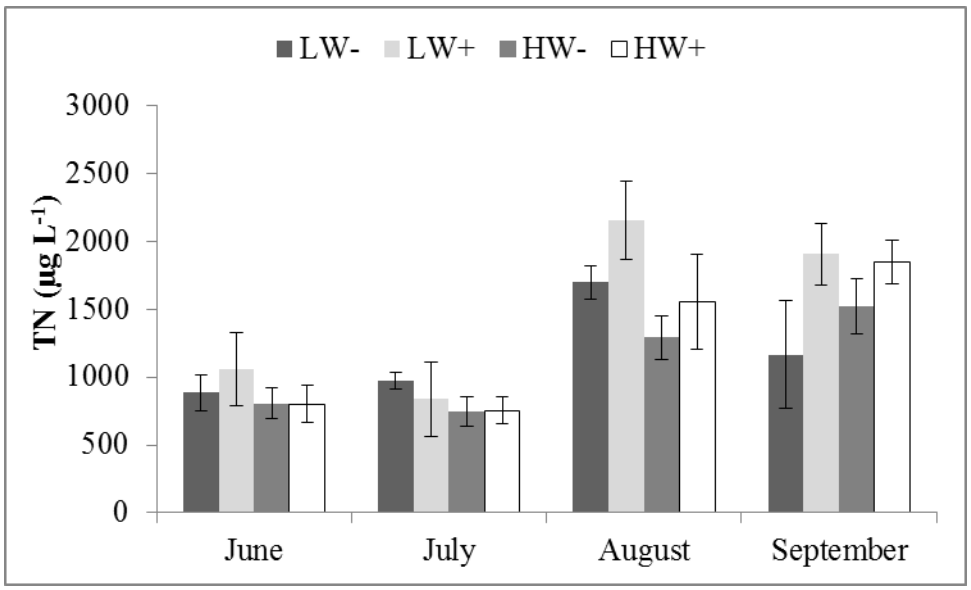


**Figure 3.3.3** Monthly mean concentrations (± 1 SD) of total nitrogen (TN) in Low water fishless (LW-), Low water with fish (LW+), High water fishless (HW-) and High water with fish (HW+) mesocosms (data taken from Bucak (2011).

### 3.3.3 Macrophytes

Water level and fish had significant effects on macrophytes PVI% (Table 3.3.1), PVI% being highest in the LW- while no significant difference was found among the HW mesocosms (Bucak, 2011). Until the September, the PVI% of the LW- mesocosms was higher than in LW+, but, following a decline in water level, the PVI% in the LW+ mesocosms started to increase and at the end of the experiment reached a level similar to that of LW- (92% PVI) (Figure 3.3.4). There was almost no macrophyte coverage in HW mesocosms (Figure 3.3.4).

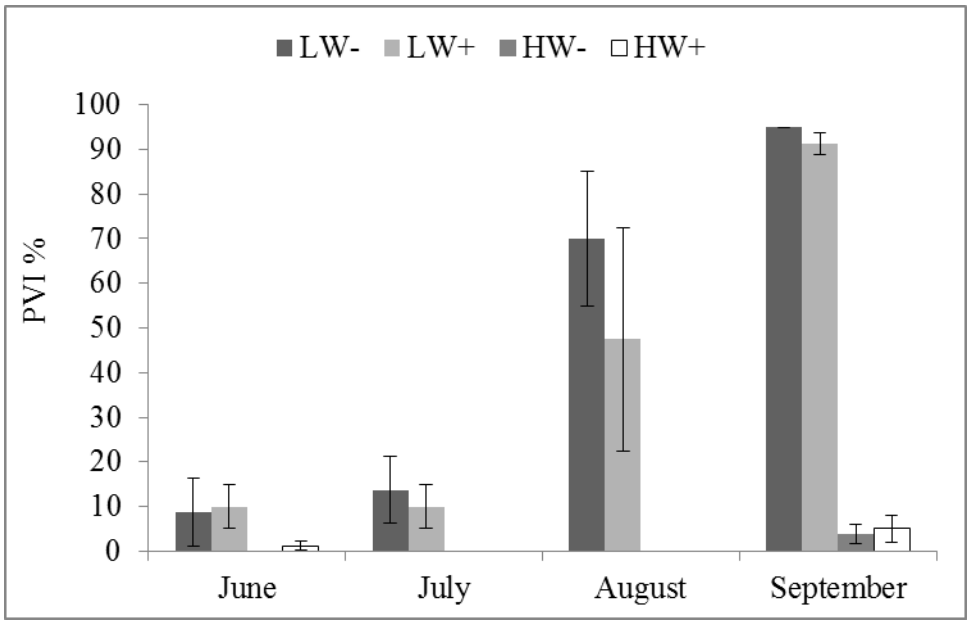


**Figure 3.3.4** Monthly PVI% (± 1 SD) in Low water fishless (LW-), Low water with fish (LW+), High water fishless (HW-) and High water with fish (HW+) mesocosms (data taken from Bucak (2011).

**Table 3.3.1:** Summary of the univariate repeated measures of two-way ANOVA testing the effect of water level and fish on nutrients and PVI%. Arrows show the direction of the treatment effect on the nutrients and PVI% (data taken from Bucak (2011).

Significance is indicated as $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, NS, not significant.

| | Water Level (WL) | Fish (F) | WL X F |
|---|---|---|---|
| TP | *** ↓ | ** ↑ | NS |
| TN | ** ↓ | ** ↑ | NS |
| PVI% | *** ↓ | *** ↑ | NS |

### 3.3.4 Biological variables

**Bacteria Biomass:** It ranged between 28 and 109 µg C $L^{-1}$ (Figure 3.3.5a). RM-ANOVA showed direct significant water level effect on bacterial biomass (Table 3.3.2). LW mesocosms overall had higher bacterial concentrations than HW (Figure 3.3.5a).

**Heterotrophic Nanoflagellates (HNF).** Its biomass ranged between 39 and 86 µg C $L^{-1}$ (Figure 3.3.5b) and significant positive effects of water level and fish interaction were observed (Figure 3.3.5b and Table 3.3.2). HNF biomass was suddenly decreased in all mesocosms in August (Figure 3.3.4b). The effect of the water level-fish interaction was not significant for the HNF: bacteria ratio while HNF:bacteria ratio was significantly lower in LW mesocosms and higher in fish treatment mesocosms (Table 3.3.2).

**Ciliates:** It's biomass ranged between 0.4 and 1.8 µg C $L^{-1}$ (Figure 3.3.5c). Oligotrichida dominated in most samples and also included the genera *Strobilidium* and *Strombidium*. RM-ANOVA showed no direct significant effect of water level on ciliate biomass, whereas a positive fish effect was recorded (Table 3.3.2). The fish

treatment had also a significant positive effect on the ciliate:bacteria biomass ratio and the ciliate:HNF biomass ratio (Table 3.3.2).

**Phytoplankton (chlorophyll-a):** It ranged between 16 and 4440 μg C $L^{-1}$ (Figure 3.3.5d) (Bucak, 2011). The phytoplankton was higher in LW+ mesocosms than other mesocosms during the study period. The water level-fish treatment interaction effect on the bacteria:phytoplankton, HNF:phytoplankton and ciliate:phytoplankton ratios was significant and negative (Table 3.3.2).

**Zooplankton:** Biomass ranged between 4 and 850 μg C $L^{-1}$ (Figure 3.3-5e) (Bucak, 2011). The zooplankton community (>140 μm) was mostly dominated by calanoid and cycloploid copepods, nauplii, *Daphnia* and small cladocerans. Copepods, cladocerans and total zooplankton biomass were pronouncedly affected by fish (Table 3.3.2, Figure 3.3.5e). RM-ANOVA showed no direct significant water level effect on zooplankton biomass, whereas a negative fish effect was recorded (Table 3.3-2). The zooplankton: phytoplankton, zooplankton: bacteria, zooplankton: HNF and zooplankton: ciliate ratios were also significantly and negatively controlled by fish (Table 3.3.2). The zooplankton: phytoplankton ratio was high in the fishless mesocosms, but low in the fish mesocosms (Figure 3.3.5h).

**Cladoceran:** Biomass ranged between 2 and 654 μg C $L^{-1}$ (Figure 3.3.5f) (Bucak, 2011). The cladoceran genera identified included *Daphnia, Megafenestra, Chydorus, Diaphanosoma, Pleuroxus, Scapholeberis, Alona*, *Ceriodaphnia*, *Bosmina* and *Macrothrix* (Bucak, 2011). A negative fish effect was recorded for cladoceran biomass (Table 3.3.2). The cladocera: phytoplankton, cladocera: bacteria, cladocera: HNF and cladocera ciliate ratios were also significantly and negatively affected by fish (Table 3.3.2). Throughout the experiment, the fishless mesocosms (LW- and HW-) were characterised by a higher contribution of cladocerans to total zooplankton biomass than those with fish.

**Copepoda:** Biomass ranged between 2 and 379 μg C $L^{-1}$ (Figure 3.3.5f) (Bucak, 2011). A negative fish effect was recorded for copepod biomass (Table 3.3-2). The copepoda: bacteria, copepoda: HNF and copepoda: ciliate ratios were also significantly and negatively affected by fish (Table 3.3.2). The interaction of water level and fish had a negative impact on the copepoda: phytoplankton ratio.

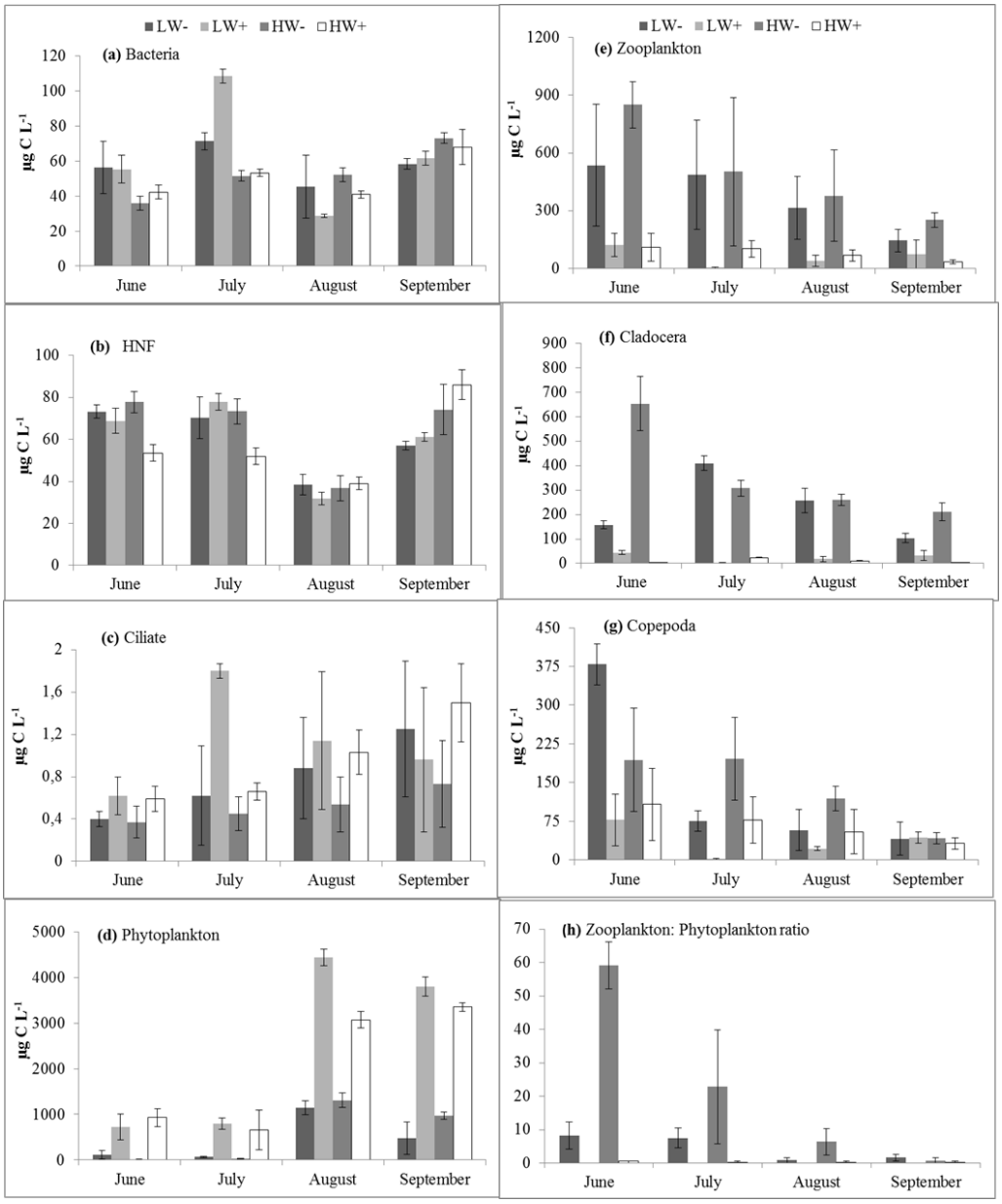


**Figure 3.3.5** Monthly biomasses (± 1 SD) of (a) bacteria, (b) HNF, (c) ciliates, (d) phytoplankton, (e) total zooplankton, (f) Cladocera, (g) Copepoda, and (h) zooplankton:phytoplankton ratio in Low Water level fishless (LW-), Low Water with fish (LW+), High Water level fishless (HW-) and High Water level with fish (HW+) mesocosms.

**Table 3.3.2:** Summary of the univariate repeated measures of two-way ANOVA testing the effect of water level and fish on biomass of microbes and other plankton. Arrows show the direction of the treatment effect on the organisms and ratios. Significance is indicated as *P < 0.05, **P < 0.01, ***P < 0.001, NS, not significant.

| | Water Level (WL) | Fish (F) | WL X F |
|---|---|---|---|
| Bacteria | *** ↓ | NS | NS |
| HNF | NS | ** ↑ | ** |
| Ciliate | NS | ** ↑ | NS |
| T. Microbial Community | ** | NS | ** ↓ |
| % T. Microbial Community | NS | ** ↓ | NS |
| Phytoplankton | * ↑ | *** ↑ | NS |
| % Phytoplankton | NS | *** ↑ | NS |
| Zooplankton | NS | ** ↓ | NS |
| % Zooplankton | NS | *** ↓ | NS |
| Cladocera | NS | ** ↓ | NS |
| Copepoda | NS | * ↓ | NS |
| All Community | NS | *** ↑ | NS |
| HNF:Bacteria | ** ↑ | * ↓ | NS |
| Ciliate:Bacteria | NS | * ↑ | NS |
| Ciliate:HNF | NS | * ↑ | NS |

**Table 3.3.2 (Continued):** Summary of the univariate repeated measures of two-way ANOVA testing the effect of water level and fish on biomass of microbes and other plankton. Arrows show the direction of the treatment effect on the organisms and ratios.
Significance is indicated as *P < 0.05, **P < 0.01, ***P < 0.001, NS, not significant.

| | Water Level (WL) | Fish (F) | WL X F |
|---|---|---|---|
| Copepoda:Bacteria | NS | * ↓ | NS |
| Copepoda:HNF | NS | * ↓ | NS |
| Copepoda:Ciliate | NS | * ↓ | NS |
| Copepoda:Phytoplankton | * | ** | * ↓ |
| Cladocera:Bacteria | NS | * ↓ | NS |
| Cladocera:HNF | NS | ** ↓ | NS |
| Cladocera:Ciliate | NS | * ↓ | NS |
| Cladocera:Phytoplankton | NS | * ↓ | NS |
| Zooplankton:Bacteria | NS | * ↓ | NS |
| Zooplankton:HNF | NS | ** ↓ | NS |
| Zooplankton:Ciliate | NS | * ↓ | NS |
| Zooplankton:Phytoplankton | NS | * ↓ | NS |
| Bacteria:Phytoplankton | *** | *** | *** ↓ |
| HNF:Phytoplankton | *** | *** | *** ↓ |
| Ciliate:Phytoplankton | * | *** | * ↓ |

### 3.3.5 Proportion of zooplankton, phytoplankton and microbial biomass.

The estimated contribution of phytoplankton to total plankton biomass was significantly higher in mesocosms with fish (Figure 3.3.6). RM-ANOVA showed no direct significant water level effect on contribution of phytoplankton whereas a positive fish effect was recorded (Table 3.3.2).

The estimated contribution of zooplankton to total plankton biomass was significantly higher in fishless mesocosms (Figure 3.3.6). RM-ANOVA showed no direct significant water level effect on contribution of phytoplankton whereas a negative fish effect was recorded (Table 3.3.2).

The estimated contribution of microbial community to total plankton biomass was significantly higher in fishless mesocosms (Figure 3.3.6). RM-ANOVA showed no direct significant water level effect on contribution of microbial community whereas a negative fish effect was recorded (Table 3.3.2).

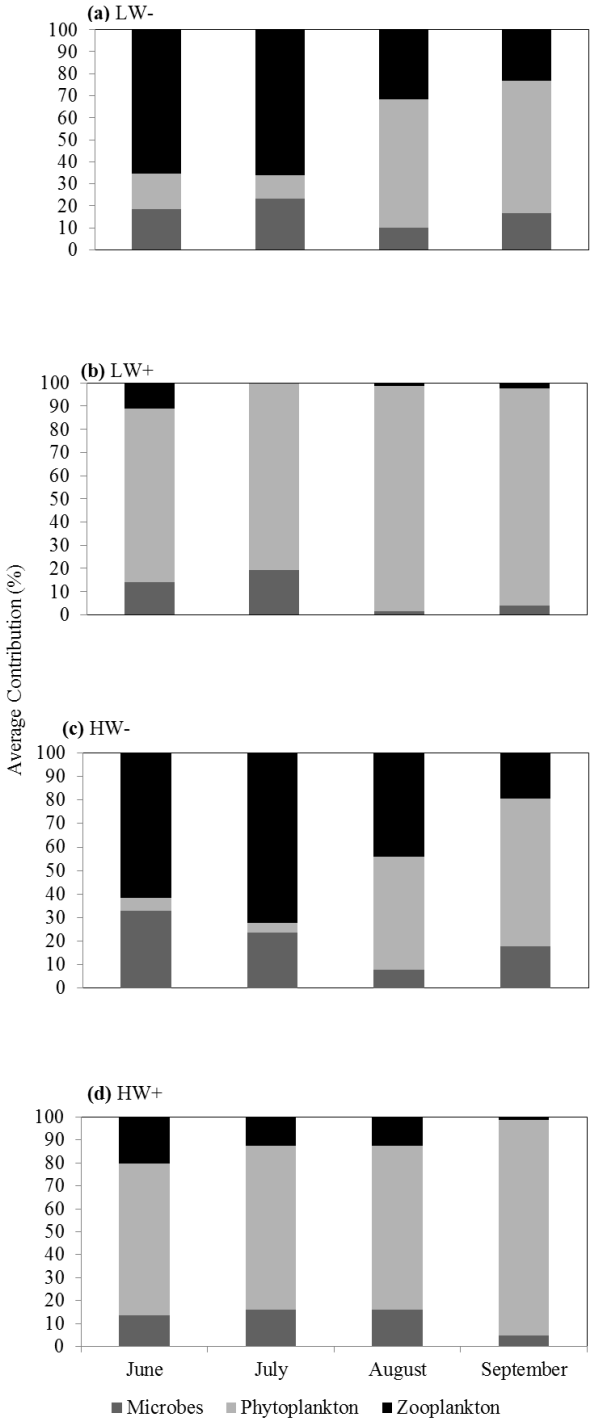


**Figure 3.3.6** Average contribution (%) of zooplankton, phytoplankton and microbes (the sum of HNF, ciliates and bacterioplankton) to total plankton biomass in Low water fishless (LW-), Low water with fish (LW+), High water fishless (HW-) and High water with fish (HW+) mesocosms**.**

## 3.4 Long-term effects of warming and nutrients on microbes and other plankton in mesocosms

### 3.4.1 Nutrients

During the experimental period the average ( ±SD) TP concentrations were 11.8 ±4.2 μg P $L^{-1}$ in ambient mesocosms and 73.3 ±11.4 μg P $L^{-1}$ in ambient enriched mesocosms, 8.5 ±3.5 μg P $L^{-1}$ in heated mesocosms and 67.3 ±46.8 μg P $L^{-1}$ in heated enriched mesocosms (Figure 3.4.1). While $PO_4$-P and TP were low in all months in the un-enriched mesocosms, TP was high throughout the period in the enriched mesocosms, exhibiting an increasing trend with time in the heated mesocosms, while $PO_4$-P declined to low levels as the season progressed.

The average TN concentrations were 0.34 ±0.32 mg N $L^{-1}$ in ambient mesocosms, 7 ±3.1 mg N $L^{-1}$ in ambient enriched mesocosms, 0.18 ±0.16 mg N $L^{-1}$ in heated mesocosms and 4.8 ±1.4 mg N $L^{-1}$ in heated enriched mesocosms (Figure 3.4.2). $NO_3$-N and TN were low in the unenriched mesocosms throughout the experiment, and both variables were high, but declined in the enriched mesocosms as the season progressed.

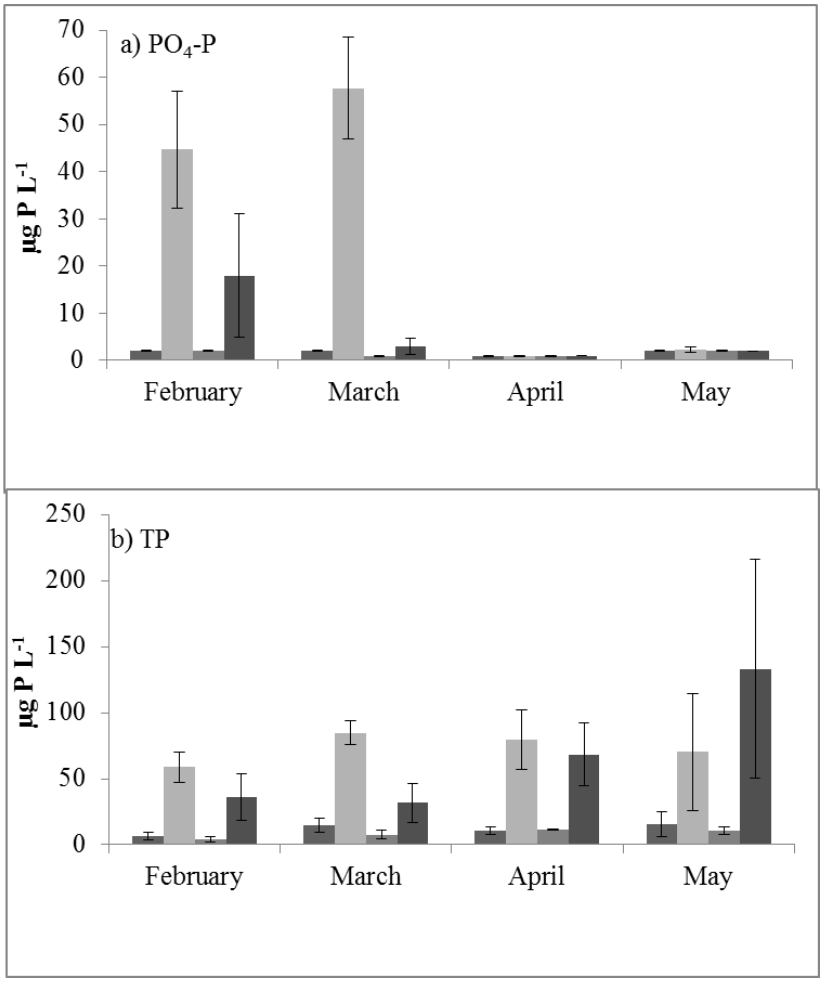


**Figure 3.4-1** Monthly mean concentrations (± 1 SD) of a) orthophosphate ($PO_4$-P), b) total phosphorus (TP), in Ambient (A), Ambient+NP (A+NP), Heated (H) and Heated+NP (H+NP) mesocosms.

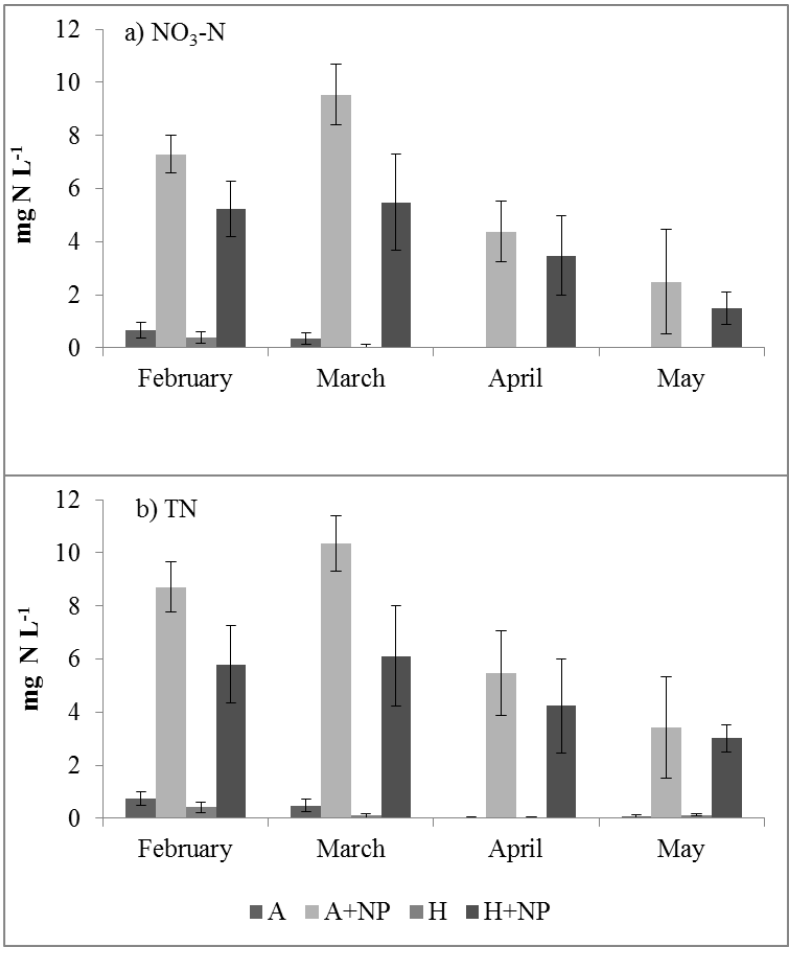


**Fig. 3.4-2** Monthly mean concentrations (± 1 SD) of a) nitrate+nitrite ($NO_3$-N) and b) total nitrogen (TN), in Ambient (A), Ambient+NP (A+NP), Heated (H) and Heated+NP (H+NP) mesocosms.

### 3.4.2 Biological variables

Biomasses of bacteria, ciliates, phytoplankton and zooplankton varied during the season as expected, with the lowest biomass occurring during the ice-covered period in winter (February and March) and the highest in spring (April and May) in all treatments (Table 3.4-1, Figure 3.4-1). Accordingly, the time effect (season) in the

RM-ANOVA´s was significant for all the response variables studied (data not shown).

### 3.4.2.1 Bacterial biomass and bacterial production (BP)

Bacterial biomass ranged between 17 and 282 µg C $L^{-1}$ (Figure 3.4-1 a). RM-ANOVA showed no direct significant warming effect on bacterial biomass, whereas an interactive positive nutrient-warming effect was recorded (Table 3.4-1).

Bacterial production (BP) increased from 22 to 616 µg C $L^{-1}$ $h^{-1}$ during the study period. RM-ANOVA revealed a significant effect of nutrient enrichment, while the effect of warming was not significant (Table 3.4-1).

### 3.4.2.2 Heterotrophic nanoflagellates (HNF)

HNF biomass ranged between 46 and 770 µg C $L^{-1}$, and a significant positive nutrient-warming interaction was observed (Figure 3.4-1 c and Table 3.4-1). The biomass of HNF was higher during the ice-covered period for H+NP and peaked in March, while for A+NP and A treatments HNF biomass peaked in April (Figure 3.3-1 c and Table 3.4-1). The effect of the nutrient-warming interaction was significant and positive for the HNF: bacteria ratio (Table 3.4-1).

### 3.4.2.3 Ciliate

Ciliate biomass ranged between 0.3 and 13.8 µg C $L^{-1}$ with maximum in spring (Figure 3.4-1 d). For the ambient, unenriched (A) treatment ciliates peaked in March and showed a hump-shaped pattern. Oligotrichida dominated in most mesocosms and included the genera *Strobilidium, Strombidium* and *Halteria*. The nutrient-warming interaction had a significant positive effect on ciliate biomass and the ciliate: bacteria biomass ratio, while no effect was found on the ciliate: HNF biomass ratio (Table 3.4-1).

### 3.4.2.4 Phytoplankton

Phytoplankton biomass ranged between 44 and 5936 μg C $L^{-1}$ (Figure 3.4-1 e). Only nutrient enrichment contributed significantly to the variation in chlorophyll-a throughout the whole study period. The nutrient-warming interaction effect on the bacteria: phytoplankton ratio was significant and negative (Table 3.4-1). No effect of nutrients or warming was observed for the HNF: phytoplankton or ciliate: phytoplankton biomass ratios (Table 3.4-1).

### 3.4.2.5 Zooplankton

Total zooplankton biomass varied between 0.2 and 174 μg C $L^{-1}$ with a maximum in May for all treatments (Figure 3.4-3 f). Nutrients positively affected total zooplankton biomass. Following ice-out, total zooplankton biomass increased in all mesocosms and the effect of nutrient enrichment became apparent (Figure 3.4-3 f). The nutrient-warming interaction had a significant negative effect on the zooplankton: phytoplankton biomass ratio and the zooplankton: HNF ratio, while no treatment effects were found on the zooplankton: ciliate biomass ratio (Table 3.4-1). Cladoceran biomass ranged from 0 to 9.1 μg C $L^{-1}$ in the monthly samples (Figure 3.4-1 g). None of the treatments significantly affected cladoceran biomass. Regardless of temperature, cladocerans dominated in the non-nutrient enriched mesocosms where *Chydorus sphaericus* (O.F. Müller) and *Bosmina longirostris* (O.F. Müller) were the most abundant species (Figure 3.4-3 g). We found a significant negative effect of nutrients on the Cladocera: phytoplankton, Cladocera: HNF and Cladocera: bacteria ratios.

Generally, copepod biomass was low, varying between 0 to 0.91 μg C $L^{-1}$ in the monthly samples (Figure 3.4-3 h). We found a significant effect of nutrients on copepod biomass. The highest biomass of copepods (cyclopoids) occurred in the ambient mesocosms (Figure 3.4-3 h). The Copepoda: bacteria, Copepoda: HNF and copepoda: phytoplankton ratios decreased significantly with increasing nutrient levels.

Total rotifer biomass ranged from 0.21 to 173 µg C $L^{-1}$ in the monthly samples (Figure 3.4-3 i). The dominant rotifer species were *Asplancha* sp. (A mesocosms), *Brachionus angularis* Gosse (A+NP), *Lepadella patella* (O.F.Müller) (H) and *Notholca squamula* (O.F. Müller) (H+NP) in February and March, whereas *Keratella quadrata* (Müller) became the dominant rotifer species in all mesocosms after ice-out. We found a significant effect of nutrients on rotifer biomass. Rotifers were the dominant zooplankter in the A+NP and H+NP mesocosms (Figure 3.4-3 i). Following ice-out, mean rotifer biomass markedly increased in all mesocosms and the effect of nutrients was significant throughout the ice-free period. We found a direct relationship between nutrients and the Rotifera: bacteria ratio and a significant positive interactive nutrient-warming effect on the Rotifera: HNF ratio. Consequently, among the mesozooplankton groups only Rotifera: HNF ratio was positively affected by warming.

The estimated contribution of phytoplankton to total plankton biomass increased at high nutrient levels, but decreased with warming, while the opposite trend was observed for the contribution to total microbial biomass (Figure 3.4-4, Table 3.4-1). Finally, no treatment differences were found for the contribution of zooplankton (Table 3.4-1).

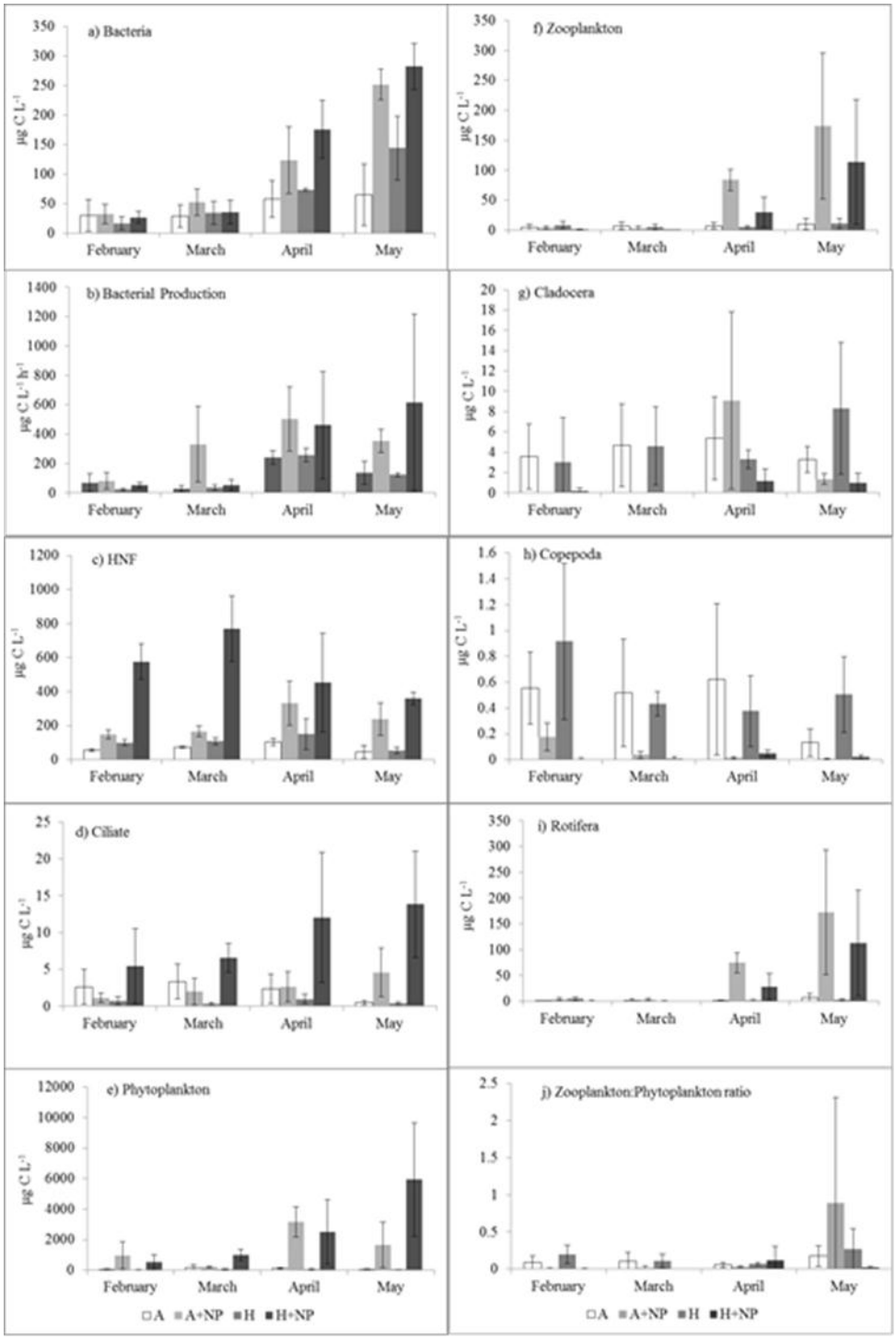


**Figure 3.4-3** Monthly biomasses (± 1 SD) of a) bacteria, c) HNF, d) ciliates, e) phytoplankton, f) total zooplankton, g) Cladocera, h) Copepoda, i) Rotifera and j) zooplankton:phytoplankton ratio and b) bacterial production in Ambient (A), Ambient+NP (A+NP), Heated (H) and Heated+NP (H+NP) mesocosms.

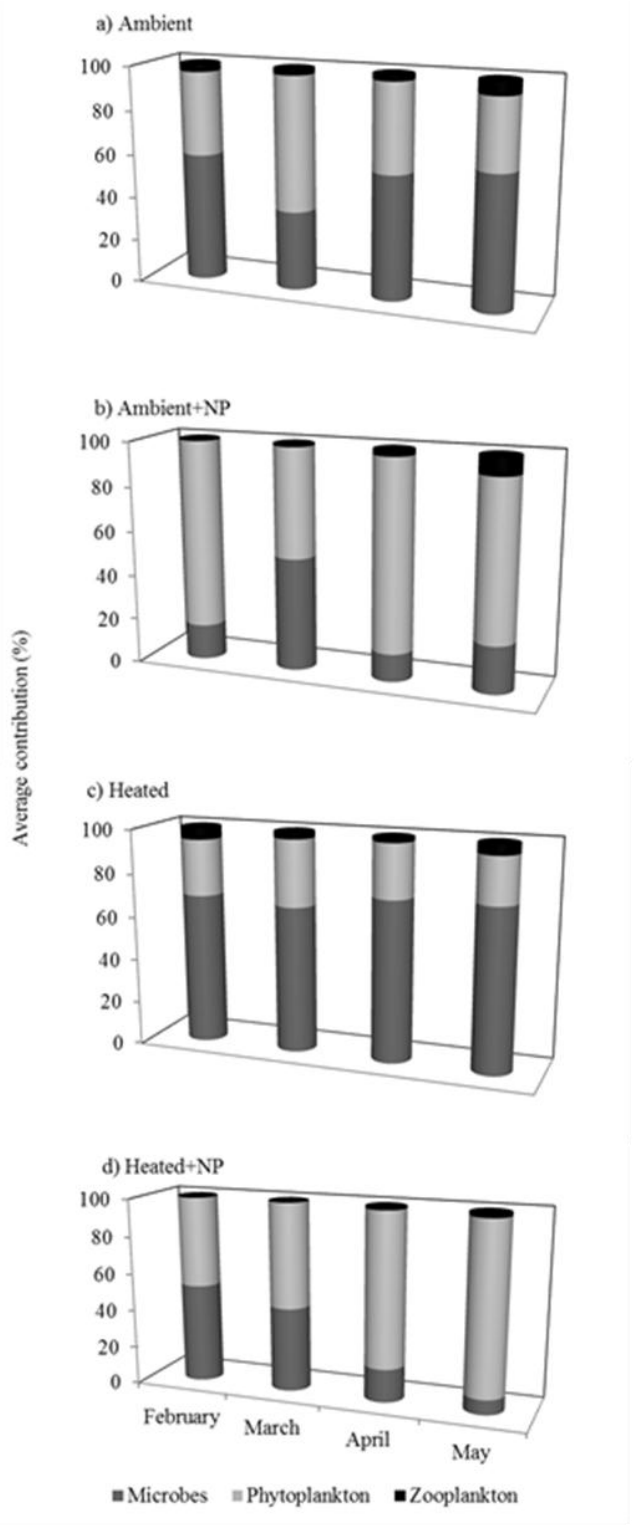


**Figure 3.4-4** Average contribution (%) of zooplankton, phytoplankton and microbes (the sum of HNF, ciliates and bacterioplankton) to total plankton biomass in Ambient, Ambient+NP, Heated and Heated+NP mesocosms (NP: nitrogen and phosphorous).

**Table 3.4-1:** Summary of the univariate repeated measures of two-way ANOVA testing the effect of warming and nutrient enrichment on biomass of microbes and other plankton. Arrows show the direction of the treatment effect on the organisms and ratios.
Significance is indicated as **P* < 0.05, ***P* < 0.01, ****P* < 0.001, NS, not significant.

| | Warming (W) | Nutrient Enrichment (NE) | W X NE |
|---|---|---|---|
| Bacteria | NS | *** | *** ⇧ |
| BP | NS | * ⇧ | NS |
| HNF | ** | *** | * ⇧ |
| Ciliate | NS | ** | ** ⇧ |
| T.Microbial Community | ** | *** | * ⇧ |
| % T.Microbial Community | * ⇧ | *** ⇩ | NS |
| Phytoplankton | NS | *** ⇧ | NS |
| % Phytoplankton | * ⇩ | *** ⇧ | NS |
| Zooplankton | NS | ** ⇧ | NS |
| % Zooplankton | NS | NS | NS |
| Cladocera | NS | NS | NS |
| Copepoda | NS | ** ⇩ | NS |
| Rotifera | NS | ** ⇧ | NS |
| All Community | NS | *** ⇧ | NS |

**Table 3.4-1:** Summary of the univariate repeated measures of two-way ANOVA testing the effect of warming and nutrient enrichment on biomass of microbes and other plankton. Arrows show the direction of the treatment effect on the organisms and ratios.
Significance is indicated as $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, NS, not significant.

| | | | |
|---|---|---|---|
| HNF:Bacteria | * | * | * ⇧ |
| Ciliate:Bacteria | NS | NS | * ⇧ |
| Ciliate:HNF | NS | NS | NS |
| Rotifera:Bacteria | NS | * ⇧ | NS |
| Rotifera:HNF | NS | NS | ** |
| Rotifera:Ciliate | NS | NS | NS |
| Copepoda:Bacteria | NS | ** ⇩ | NS |
| Copepoda:HNF | NS | ** ⇩ | NS |
| Copepoda:Ciliate | NS | NS | NS |
| Copepoda:Phytoplankton | NS | ** ⇩ | NS |
| Cladocera:Bacteria | NS | * ⇩ | NS |
| Cladocera:HNF | NS | * ⇩ | NS |
| Cladocera:Ciliate | NS | NS | NS |
| Cladocera:Phytoplankton | NS | * ⇩ | NS |
| Cladocera:Ciliate | NS | NS | NS |
| Zooplankton:Bacteria | NS | NS | NS |
| Zooplankton:HNF | *** | *** | *** ⇩ |
| Zooplankton:Ciliate | NS | NS | NS |
| Zooplankton:Phytoplankton | ** | ** | *** ⇩ |
| Bacteria:Phytoplankton | NS | ** | * ⇩ |
| HNF: Phytoplankton | NS | NS | NS |
| Ciliate:Phytoplankton | NS | NS | NS |

# CHAPTER 4

# DISCUSSION

## 4.1. Role of top down and bottom up controls on microbial food webs of Some Turkish Shallow Lakes

Our key findings were: (i) Nutrient (bottom-up control) had a significant effect on the biomass of the microbial community in studied lakes: bacteria and HNF increased with increasing nutrients whereas ciliate decreased, (ii) Top-down control of cladocerans on microbial loop, HNF on bacteria and ciliate on HNF decreased with increasing nutrients, iii) Macrophytes had a significant impact on microbial community members: bacteria and HNF biomasses decreased and ciliate biomass increased with increasing PVI%. (iv) Our results from both snap shot sampling and in situ grazing experiment revealed that the different zooplankton composition had different cascading effect on microbial community members, (v) Temperature had a positive impact on the biomasses of bacteria and HNF, vi) There were no differences for microbial community biomass between the pelagic and littoral zones of lakes.

### 4.1.1 Bottom-up and top-down control

The overall nutrient concentrations were higher in cluster 1 and 3 and the response of microbial community members to increasing nutrient levels was different in studied lakes: bacteria and HNF biomasses increased with increasing nutrients whereas ciliate decreased (Gilbert & Jack; 1993; Smith & Prairie, 2004; Nelson & Carlson,

2008). Biomass and abundance of all organisms in the pelagic habitat increases with nutrient enrichment. (Pace, 1986; Berninger *et al.,* 1991), but each group response to increasing nutrients differ (Christoffersen *et al.,* 1993; Gasol & Vaque´, 1993; Jansson *et al.,* 1996). Thus, the structure of the pelagic community and interactions among organisms might be influenced by nutrient enrichment

RDA results revealed that bacteria biomasses were positively related with TN and bacteria biomasses were higher in cluster 1 and 3 lakes where TN concentrations were higher than clıuster 2 lakes. However, bacteria biomass was significantly higher in Lake K.Akgöl (northern lakes) and Gebekirse (southern lakes) where the TN values were higher. All of these results support the idea that primary production increass with N availability (Faithfull *et al.,* 2011).

In the study of Jeppesen *et al*. (1997), it was observed that "Top-down control of large cladocerans on bacteria was weak at high nutrient concentrations in northern European shallow lakes because of the disappearance of these cladocerans due to higher predation on macrozooplankton with increasing trophic state". Moreover, Conty *et al.,* (2007) showed that "Top down control by cladocerans was weaker in some eutrophic shallow Spanish lakes than previously shown in northern European shallow lakes (Jeppesen *et al.,* 1997) and rotifers were the important predators of bacteria in these lakes". In accordance with these studies, our results demonstrate that the top down control of Cladocera on microbial loop decreases with increasing nutrient levels (lowest cladocera in cluster 3 which had highest TN concentrations) whereas rotifera grazing can have a strong control on microbial loop with increasing nutrient concentrations (higher rotifera biomass in cluster 1 and 3).

HNF biomasses were higher in cluster 3 lakes with highest TN concentrations.This could be because of decreased grazing pressure by ciliates (lowest ciliate biomass in cluster 3) and increase in bacterial biomass with increasing nutrients (higher bacteria biomass in cluster 3) (Nelson & Carlson, 2008; Faithfull *et al.,* 2011). Ciliate

biomasses were lower or zero in cluster 3 lakes Rotifera biomass were higher in cluster 1 and 3 lakes where TN concentrations were higher. Stepwise regression results showed that rotifera: ciliate ratio was significantly positively correlated with TN concentrations. This may be explained by the fact that rotifera can be efficient predator on ciliates (Pernthaler *et al.,* 1996; Tadonleke *et al.,* 2004) and rotifera become dominant species and their top down effect on ciliates increases due to eutrophication (Gilbert, 1980; Arndt, 1993; Gilbert & Jack, 1993).

The contribution of microbial community to plankton community was higher than phytoplankton in southern lakes. This might be related with inedible cyanobacteria was dominated southern lakes in relation with higher nutrients that may have limited zooplankton biomass thus indirectly effecting the microbial community (Johnk *et al*., 2008; Huber, Adrian & Gerten, 2008; Jeppesen *et al*., 2009).

Higher nutrient concentrations might suppress plant development in lower latitudes (Becares *et al.,* 2008). Our results supported this. In lake cluster 3 (southern lakes: Gölcük Ödemiş, Gebekirse, Saklıgöl and Baldımaz) there were no plants in this lakes since the TN concentrations were higher than other clusters in cluster 3.

RDA analysis and stepwise multiple regression showed a negative correlation between bacteria biomass and PVI. In accordance with these bacteria biomasses were lowest in lake cluster 2 where the PVI% of lakes was highest. These results support the idea that allelopathic effect of the macrophytes had a adverse effect on the production of bacteria (Stanley *et al.,* 2003).

RDA analysis also revealed that there was a negative relationship between HNF biomass and PVI%. Stepwise multiple regression results confirmed a positive correlation between ciliate: HNF ratio and PVI% and negative correlation between bacteria biomass and PVI%. Thus, higher grazing pressure of ciliates (top down effect) and lower bacteria biomasses (bottom up effect) with high PVI% values

might be the reason for low HNF biomasses in clusters 1 and 2 (Mieczan, 2008 and 2010; Stanley *et al.,* 2003).

The contributions of microbes to plankton community were higher in Lakes K.Akgöl, Gölcük-Ödemiş, Gebekirse, Saklıgöl and Baldımaz where there were rare or no macrophytes. These results were in accordance with the study of Zingel and Nöges (2008) which showed that the contribution of microbial loop weakened in dominance of macrophytes in lakes. Mieczan (2008 and 2010) found that "The abundance and biomass of ciliates were significantly higher at sites with structurally most complex plants than in the open water or sparsely vegetated sites and ciliates probably use macrophyte vegetation as potential refuge to avoid predation pressure". In accordance with this, ciliate biomasses were highly correlated with PVI according to RDA analysis and stepwise multiple regression. Field observations also showed that there were rare or no ciliates in cluster 3 lakes where there were rare or no macrophytes.

Tavsanoglu et al., (2012), suggest that " *Daphnia* in Mediterranean shallow lakes avoid submerged macrophytes and instead prefer to hide near the sediment when exposed to predation risk, as also observed in subtropical shallow lakes". In accordance with this, Cladocera biomasses were lower in cluster 2 lakes where the PVI% was higher. As a consequence of this, ciliates become free from zooplankton predation pressure (higher ciliate biomass in cluster 2) and increasing ciliate grazing on HNF resulted with higher bacteria biomass

The different zooplankton composition had different cascading effect on microbial community members (Gilbert, 1980; Arndt, 1993; Gilbert & Jack, 1993;Burn & Schallenberg, 1996; Sommer *et al.,* 2003). Ciliate biomasses were lower in cluster 3 lakes where the rotifera was dominant taxa, bacteria and HNF biomasses were lower in cluster 2 lakes where cladoceran and copeod biomasses were higher. The effects of different zooplankton groups was discussed in detail in the in situ experiment.

To sum up, the different response of microbial loop community to increasing nutrient levels may be explained by changing top down control within microbial loop (Rae & Vincent 1998; Christoffersen *et al.,* 2006), the direct and indirect impact of different zooplankton groups on microbial loop (Porter & McDonough, 1984; Nõges *et al.,* 1998; Jürgens & Jeppesen, 2000).

### 4.1.2 In situ grazing experiment

There is an increasing effort to understand the impact of different zooplankton groups on microbial community since they are a good food resource for different zooplankton groups (Sanders *et al.,* 1989; Vaque *et al.,* 1992; Arndt, 1993; Jürgens, 1994; Hwang & Heath, 1999; Balseiro *et al.,* 2001, Modenutti *et al.,* 2003). We observed that different zooplankton taxa, zooplankton composition and zooplankton biomass had a different cascading effect on bacteria, HNF and ciliates in in situ grazing experiments as it observed in different mesocosm experiments (Wickham, 1998; Modenutti et al., 2003; Agasild & Nöges, 2005; Sinistro et al., 2007).

Nested ANOVA results showed that there was no regional difference between lakes but the variation was due to the different zooplankton composition and biomass exerted different grazing pressure in lakes.

There was no ciliate after 24 h incubation in zooplankton treatment bottles in all lake clusters and this supported the previous findings that all zooplankton taxa can graze on ciliates: small cladocera (*Bosmina longirostris* (O. F. Müller, 1776) and *Chydorus sphaericus*), (Jurgens, Arndt & Zimmermann, 1997; Marchessault & Mazumder, 1997), large cladocera (*Daphnia spp.)*, calanoid and cyclopoid copepoda copepoda (Burns & Gilbert, 1993; Wiackowski et al., 1994; Wickham, 1995), rotifera (Gilbert, 1980; Arndt, 1993; Gilbert & Jack, 1993, Sommer *et al.,* 2003).

HNF biomass increased in clusters 1 and 2 in zooplankton (Z) treatments compared to control (NZ). This may be related with indirect positive effect of zooplankton by reducing ciliate grazing on HNF (Modunetti *et al.,* 2003; Sommer *et al.,* 2003).

HNF biomass decreased in cluster 3 in zooplankton treatment. This might be related with the zooplankton grazing on HNF. In Lake Yayla where the rotifera was the dominant group revealed that rotifera also graze on HNF as ciliates biomass was very low. However higher contribution of rotifer to total zooplankton biomass in clusters 3 might be the reason for low HNF biomass. These results support the idea that rotifera can be efficient predator on ciliates as well as HNF (Pernthaler *et al.,* 1996; Tadonleke *et al.,* 2004). Zooplankton grazing impact on HNF was observed in lake Saklı. Since there was no ciliate, HNF might became an alternative food resource for cladocera (Wickham,1993), cyclopoid copepod (Sommer *et al.,* 2003) and rotifera (Arndt, 1993) in this lake. In Lake Poyrazlar, *Diaphonosoma birgei*, (Korinek, 1981) was the dominat species and was also able to grazed on HNF (Wickham,1993). However, higher contribution of large cladocera (*Daphnia spp*) to total zooplankton biomass may explain the low biomass of HNF in cluster 3 lakes since large cladocera can graze on HNF as well as ciliates (Müller *et al.,* 1991, Weisse, 1991; Carrick *et al.,* 1991; Christoffersen *et al.,* 1993; Burn & Schallenberg, 1996; Modenutti *et al.,* 2003).

Higher increase in the biomass of bacteria in control treatment and no change in zooplankton treatment revealed a grazing impact of zooplankton on bacteria in cluster 2 where the large cladocera (*Daphnia spp*.) biomass was highest among the clusters and they can graze on bacteria (Jeppesen *et al.,* 1992; Modenutti *et al.,* 2003).

No top-down control of ciliates on HNF affected bacterial biomass by altering the grazing pressure on bacteria (Markosova & Jezek, 1993; Riemann, 1985) and might be the reason for lower bacteria biomasses and higher HNF biomass in zooplankton

treatments (Jurgens *et al.*,2000; Kisand *et al.,* 2000; Simek *et al.,* 2000). In-situ grazing experiment results support the previous findings that HNF were mainly responsible for bacterial biomass control (Fenchel 1982; Giide 1986; Pernthaler *et al.,* 1996; Sanders *et al.,* 2000; Callieri *et al.,* 2002) and ciliates strongly grazed on HNF in studied lakes (Sanders *et al.,* 1989, Simek *et al.,* 1990; Weisse *et al.,* 1990; Sherr *et al.,* 1991; Kivi & Setela, 1995; Szelag-Wasielewska & Fyda 1999).

### 4.1.3 Temperature

Savage *et al.,* (2004) showed that "Many biological processes, such as the growth and production of microbial organisms, are positively related to temperature", "but a stimulation of growth may not necessarily lead to a net increase in biomass due to counteracting effects, such as elevated predation (Rae & Vincent 1998; Christoffersen *et al*., 2006).

RDA results revealed that bacteria and HNF biomasses were mainly regulated by temperature. Stepwise multiple regression also showed a positive correlation for bacteria and HNF biomasses. However, bacteria and HNF biomasses relatively higher in cluster 3 which was consist of high temperature lakes. These results are consistent with some mesocosms experiments from Denmark which showed a significant effect of temperature on increase in bacteria and HNF biomass (Christoffersen *et al*., 2006; Özen *et al*., in press).

Stepwise multiple regression results confirmed a negative impact of temperature with the zooplankton grazing pressure on microbial community members. However, in cluster 3 which consist of highest temperature lakes, there were least cladocera and Copepoda among the lake clusters. This might be explained with high planktivorous fish biomass, higher grazing pressure on zooplankton, (Jeppesen *et al*., 2009, 2010) and higher nutrient concentrations through warming induced eutrophication in southern lakes can induce higher fish predation (Jeppesen *et al.,* 2009, 2010).

### 4.1.4 Habitat choice: Pelagic littoral difference

Our results demonstrate that there were no differences for the bacteria biomass between the pelagic and littoral zones of lakes in contrast to some studies that showed that more bacteria were found in the pelagic zone of lakes than the littoral zone in Brazilian Lakes (Haig-They *et al.,* 2010), in Chinese lakes (Wu *et al.,* 2007) and in North temperate lakes (Sondergaard *et al.,* 1997) and some studies showed that there were more bacteria in the littoral zone of lakes due to higher productivity (Wetzel & Søndergaard, 1998; Buesing & Gessner, 2006, Filippini *et al.,* 2008). The indifference of the bacteria biomass between pelagic and littoral zones might be related with the areas of studied 14 lakes (varied between 1 and 400 hectare) since the difference between littoral and pelagic in bacteria biomass increased with lake area (Haig-They *et al.,* 2010).

There were rare or no plants in 2 of 7 northern lakes (K.Akgöl and Taşkısığı), whereas there were rare or no plants in 4 of 7 southern lakes (Gölcük Ödemiş, Gebekirse, Saklıgöl and Baldımaz). The horizontal heterogenity in bacterial biomass is associated with the presence of plants (Wu *et al.,* 2007). The absence of plants may also cause the indifference between pelagic and littoral zones of microbial and zooplankton communities of these 6 lakes since plant density may influence the ecology and water biochemistry of lakes (Chambers *et al.,* 2008), offer a shelter from predators to many organisms such as young fish and zooplankton (Scheffer, 1998; Nurminen *et al.,* 2007), serve food source for phytoplankton and bacteria (Kuczyńska-Kippen, 2005; Vieira *et al.,* 2007; Tessier *et al.,* 2008).

### 4.1.5 Conclusion

Our results showed that there were differences between lakes for microbial community due to different nutrient concentrations (especially TN), temperature differences and plant coverage. Our results showed that top down control of

cladocera and copepoda was higher in lakes with low TN, medium temperature and high plants and bottom up control was higher in lakes with higher TN concentrations, low or no plant covarage and higher bacteria biomass. These differences between Turkish lakes showed that global warming may also effect the relation between top down and bottom up factors in our region. Consequently, the effects of warming may be strongest in our region in the future. Warming may exacerbates eutrophication (Özen *et al.,* 2010; Jeppesen *et al.,* 2009, 2011) and in a consequence of that further stimulate changes may occur in the microbial as well as the classical aquatic food web and their interactions.

## 4.2. The relative importance of microbial communities in the planktonic food web of Lakes Eymir and Mogan 2010–2011

### 4.2.1. The relative importance of microbial communities in the planktonic food web of Lakes Mogan

Our results demonstrate that change in the concentrations of nutrients (as a bottom-up control) and zooplankton biomass and composition (as a top-down control) between 2010 and 2011 were the main factors that regulate microbial community in Lake Mogan. However decreasing fish biomass and PVI% in 2011 were the indirect factors that may affect microbial community.

Bacteria and ciliate biomasses were higher in 2010 with higher nutrient levels, which give a boost to the microbial community as it observed in many eutrophic lakes (Pace, 1986; Berninger *et al.,* 1991; Christoffersen *et al.,* 1993; Gasol & Vaque´, 1993; Jansson *et al.,* 1996), while the biomass of heterotrophic flagellates did not differ between years. Although the biomass of microbial community was lower in 2011 with lower nutrients, their contribution to plankton community increased in 2011. These results in our study were in accordance with other studies that report

higher contributions of microbial food web in lakes of lower productivity (Hwang & Heath, 1997) and decreasing importance of the microbial loop with increasing productivity of the system (Porter *et al.*, 1988; Weisse, 1991, Azam & Smith, 1991).

Competition for nutrients may be a critical aspect of bacteria-phytoplankton interactions in Lake Mogan since they compete for the same resources (TP and TN) (Cotner, 1992; Elser & George, 1995; Brett *et al*., 1999). Both bacterial biomass and phytoplankton biomass decreased in 2011 in Lake Mogan with decreasing nutrients. However, bacteria: phytoplankton ratio was significantly higher in 2011 and this might be related with cladoceran grazing on phytoplankton. Since zooplankton: phytoplankton and cladoceran: phytoplankton ratios were higher in 2011 (though no annual differences for copepod: phytoplankton and rotifer: phytoplankton ratios) and there were more nutrients in 2010, we may conclude that phytoplankton biomass was controlled by nutrients in 2010 and by zooplankton especially cladocerans in 2011. Changes in phytoplankton biomass by zooplankton grazing might indirectly affect the bacterial biomass in Lake Mogan since exudates produced by phytoplankton are an important organic substrate for bacteria in many aquatic ecosystems (Wheeler & Kirchman 1986; Baines *et al*., 1991; Sundh., 1992; Kirchman 1994).

Higher nutrient concentrations in 2010 and lower HNF: bacteria ratio suggested that weak or no coupling of HNF and bacteria in more eutrophic systems as suggested by other studies (Gasol & Vaque´, 1993; Tzaras & Pick, 1994; Wieltschnig *et al.*, 2001). However, higher HNF: bacteria ratio and lower ciliate:HNF ratio in 2011 suggested that HNF biomass regulated prey population not being controlled by the ciliates predation. This result showed that heterotrophic nanoflagellates were important for controlling bacterial biomass control in 2011 (Fenchel 1982; Giide 1986; Pernthaler *et al*., 1996; Sanders *et al*., 2000; Callieri *et al.*, 2002).

In 2010, ciliates in Lake Mogan were mostly exposed to grazing pressure of calanoid copepods that known to be efficient selective grazers of ciliates (Burns & Gilbert,

1993; Wiackowski *et al.*, 1994; Wickham, 1995). In 2011, both calanoid copepods and small cladocerans [*Diaphanosoma lacustris* (Korinek) and *Chydorus sphaericus* (O.F. Müller)] grazed on ciliates as they are efficient ciliate grazers (Demott, 1985; Jurgens, Arndt & Zimmermann, 1997; Marchessault, 1997). The higher zooplankton biomass in 2011 might explained the lower ciliate biomass and its cascading effect on HNF and bacteria in Lake Mogan.

Strong predation effect of fish on zooplankton might have resulted in lower biomass of copepods and cladocerans in Lake Mogan in 2010 with relatively higher fish biomass (Brooks & Dodson, 1965 Gliwicz, 2003; Jeppesen *et al*., 2008; Schulze, 2011). Fish-mediated trophic cascades on microbial loop processes might be the reason for the annual differences for the microbial communities of Lake Mogan since it is a predominating factor found elsewhere (Riemann, 1985; Pace & Funke, 1991; Pace & Cole; 1996). More abundant plankti-benthivorous fish may enhance predatory control of zooplankton (Jeppesen *et al.*, 2009, 2010) with cascading effects on bacteria, and protozoans (Porter & McDonough, 1984; Nõges *et al*., 1998; Jürgens & Jeppesen, 2000). Ciliate biomasses were lower in both pelagic and littoral zones of Lake Mogan in 2011 whereas cladoceran and copepod increased due to lower predation impact of fish. Lower top-down control of ciliates on HNF affected bacterial biomass and production by altering the grazing pressure on bacteria (Markosova & Jezek, 1993; Riemann, 1985) and might be the reason for lower bacteria biomasses and higher HNF:bacteria ratio in 2011 (Jurgens *et al*.,2000; Kisand *et al.*, 2000; Simek *et al*., 2000).

Significant habitat difference was only observed for bacteria biomass. The bacterial biomass was significantly higher in pelagic zone of Lake Mogan than the littoral zone in both years. The horizontal heterogeneity in bacterial biomass in Lake Mogan might be associated with the presence of plants (Wetzel & Søndergaard, 1998; Wilcock *et al.*, 1999; Stanley *et al.*, 2003; Wu *et al.*, 2007) and the negative allelopathic effect of the plants on the production of bacteria.(Stanley *et al.*, 2003).

Muylaert *et al.* (2002) stated that "The combination and the importance as structuring forces of top-down and bottom-up controls show seasonal variations that play an important role in the structure and dynamics of the bacterial community for eutrophic lakes". The effect of seasonality was observed for bacteria, HNF and phytoplankton. Structural and functional changes in the both microbial food web (Jurgens *et al.*, 2000) and phytoplankton (Christoffersen et al., 1993) are expected due to seasonal changes in zooplankton composition. In autumn 2010, increased grazing control of zooplankton on ciliate (higher cladocera, copepoda and rotifers biomass in autumn 2010) was resulted higher grazing pressure of HNF on bacteria and resulted with lower bacteria biomass in autumn 2010. Winter bacterial biomass was significantly higher in 2011 in spite of the decrease in nutrient concentrations. This may be related with decreasing grazing pressure of HNF since HNF: bacteria ratio was significantly lower in winter 2011 than the other seasons and HNF were important for bacterial biomass control in shallow lakes (Fenchel 1982; Giide 1986; Pernthaler *et al*., 1996; Sanders *et al*., 2000; Callieri *et al*., 2002; Adamczewski *et al.*, 2010). Rotifer was dominant in autumn 2011 in Lake Mogan and both bacteria and HNF biomass decreased. Ciliate biomasses were decreased in winter 2010 and autumn 2011 when rotifer was dominant taxa. All these results showed that rotifer can graze on bacteria (Starkweather *et al.*, 1979; Bogdan *et al.*, 1980; Boon & Shiel, 1990) HNF (Pernthaler *et al.*, 1996; Tadonleke *et al.*, 2004) and ciliates (Gilbert, 1980; Arndt, 1993; Gilbert & Jack, 1993).

### 4.2.2. The relative importance of microbial communities in the planktonic food web of Lake Eymir

Our results demonstrate that change in the water depth and change in concentrations of nutrients during the sampling period had a different effect on the components of the classical and microbial components of food web in Lake Eymir.

Higher concentrations of both TP and TN in 2010 can be attributed to up-concentration in the low water level due to evaporation in 2010 (Özen *et al.,* 2010; Bucak *et al*., 2012). Microbial community responded reduction in nutrients in an opposite way and contribution of microbial community increased in 2011. These results were in accordance with other studies that report higher proportions of microbes in lakes with lower nutrient availability (Hwang & Heath, 1997, Fahnenstiel *et al.,* 1998, Biddanda *et al.,* 2001, Cotner & Biddanda, 2002) and decreasing importance of the microbial food web with increasing productivity of the system (Porter *et al.,* 1988; Weisse, 1991, Azam & Smith, 1991, Biddanda & Cotner, 2001).

Nutrient might be a critical aspect of bacteria-phytoplankton interactions in Lake Eymir. Nutrient addition experiments in Lake Castle showed that both phytoplankton and bacteria were limited by phosphorous and nitrogen explained a generous proportion of variability for bacteria and phytoplankton biomass and competition for nutrients were important for bacteria and phytoplankton interactions (Brett *et al.,* 1999). Thus, decrease in nutrients in 2011 might explain the decrease in bacteria and phytoplankton biomass in 2011.

Although there were no statistically significant annual differences for top down control of zooplankton on microbial community (zooplankton:bacteria, zooplankton:HNF, zooplankton:ciliate) and ciliates on HNF (ciliate:HNF ratio), HNF:bacteria ratios were lower in 2010 than 2011 in Lake Eymir where nutrient concentrations were higher in 2010 than 2011. This finding supports the idea that that weak or no coupling of HNF and bacteria under eutrophic conditions compared to oligotrophic systems (Gasol & Vaque, 1993; Tzaras & Pick, 1994; Wieltschnig et al., 2001).

In 2011, copepod: HNF ratio was significantly lower this led to a significantly higher biomass of HNF and low bacteria biomass that heterotrophic nanoflagellates were

important for controlling bacterial biomass in 2011 as reported in other studies (Fenchel 1982; Giide 1986; Pernthaler et al., 1996; Sanders et al., 2000; Callieri et al., 2002). However, our results also revealed that *Daphnia spp.* may also play key roles in the bacterial microbial community biomass control by directly grazing on bacteria as reported elsewhere (Riemann, 1985; Christoffersen *et al*., 1993) since the dominant taxa was mostly cladocerans (mainly *Daphnia magna* and *Daphnia pulex*) in both 2010 and 2011, cladoceran grazing on bacteria was higher in 2011 as probably *D.magna* was dominant in 2011 and beinng a very effcient grzaer of bacteria (Riemann, 1985; Christoffersen *et al*., 1993). This may also be related with the low phytoplankton biomass and cladocerans may have grazed on bacteria as an alternative food source (Jürgens,1994; Kamjunke *et al*., 1999). *Daphnia spp.* might also indirectly affect bacteria biomass by grazing on HNF and ciliates and changing top down control of HNF on bacteria (Porter *et al*., 1988; Jürgens, 1994) since cladocera was dominated by *Daphnia spp.* in 2010 and in winter and spring of 2011.

Increasing water level may suppress the macrophyte growth and it may indirectly affect microbial community. There were less bacteria biomass in littoral zone and bacterial biomass was increased in littoral zone when there were no submerged plants in 2011. This result was in accordance with some previous studies (Jurgens & Jeppesen, 2000; Stanley *et al*., 2003) and supported the idea that allelopathic effect of plants had adverse effects on the production of bacteria. (Stanley *et al*., 2003).

Muylaert *et al.* (2002) stated that "The effect of top-down and bottom-up controls show seasonal variations that play an important role in the structure and dynamics of the bacterial community for eutrophic lakes" There was a increase in TP in autumn 2010 and it was resulted with increasing bacteria biomass. Seasonal change in the composition of zooplankton also effected the grazing pressure of zooplankton on microbial community (Christoffersen *et al*., 1993; Jurgens *et al.,* 2000). Rotifers were dominant taxa in winter 2010 and autumn 2011 and the biomasses of bacteria and ciliates decreased since rotifers can graze down on bacteria efficiently

(Starkweather *et al*., 1979; Bogdan *et al*., 1980; Boon & Shiel, 1990).

Since the *Daphnia spp.* were dominant in other seasons and they can grazed on all microbial community, microbial biomass were lower during the study period (Riemann, 1985; Porter *et al*., 1988; Christoffersen *et al*., 1993; Jürgens, 1994).

### 4.2.3 Comparison between Lakes Mogan and Eymir

Results from Lakes Mogan and Eymir were in accordance with other studies that report higher proportions of microbes in lakes with lower nutrient availability (Hwang & Heath, 1997, Fahnenstiel et *al.*, 1998, Biddanda *et al.*, 2001, Cotner & Biddanda, 2002) and decreasing importance of the microbial food web with increasing productivity of the system (Porter *et al.*, 1988; Weisse, 1991, Azam & Smith, 1991, Biddanda & Cotner, 2001). In both lakes, HNF:bacteria ratios were lower in 2010 than 2011 when nutrient concentrations were higher in 2010. This finding supports the idea that that weak or no coupling of HNF and bacteria under eutrophic conditions compared to oligotrophic systems (Gasol & Vaque, 1993; Tzaras & Pick, 1994; Wieltschnig *et al.*, 2001). The results of both lakes showed that heterotrophic nanoflagellates were important for controlling bacterial biomass in 2011 as reported in other studies (Fenchel 1982; Giide 1986; Pernthaler *et al*., 1996; Sanders *et al*., 2000; Callieri *et al.*, 2002).

In Lake Eymir, cladoceran biomass was significantly higher than that of Lake Mogan in both years since there was not a strong predation pressure of fish. The overall bacteria and HNF biomasses were lower in Lake Eymir than in Lake Mogan probably due to higher grazing impact of large body sized daphnids such as *D. magna*, since it is an efficient grazer on all components of the microbial community (Jürgens & Stolpe, 1995; Gasol *et al.*, 1995).

In both lakes , the ciliates were main grazers of HNF as recorded elsewhere ( Sherr *et al.,* 1991, Szelag-Wasielewska & Fyda 1999; Premke & Arndt, 2000; Zingel *et al.,* 2007).

Results from both lakes showed that competition for nutrients may be a critical aspect of bacteria-phytoplankton interactions (Cotner, 1992; Elser & George, 1995; Brett *et al*., 1999) and both bacteria and phytoplankton biomasses were regulated by cladocerans (Cyr & Pace, 1992; Jürgens, 1994; Jürgens & Jeppesen, 2000). Results from both lakes showed the negative effect of macrophytes on the production of bacteria due to allelopathic effect of the macrophytes and less bacteria biomass in the littoral habitat of both lakes than the pelagic habitats of both lakes (Stanley *et al.,* 2003) but the effect was more clear in Lake Mogan since the PVI% was higher than that of lake Eymir.

Structural and functional changes in the both microbial food web (Jurgens *et al.,* 2000) and phytoplankton (Christoffersen *et al.,* 1993) were observed in both lakes due to seasonal changes in zooplankton composition as it discussed separately in the text before.

### 4.2.4. Conclusion

In conclusion, the dynamics of the microbial and planktonic food web were regulated both by bottom-up and top-down mechanisms in Lake Mogan since there were annual differences for nutrients and HNF, ciliate and zooplankton biomasses. Bottom-up control (nutrients) seem to be of major importance for the dynamics of the microbial and planktonic food web in Lake Eymir. The effect of fish on zooplankton and effect of macrophytes were more effective in Lake Mogan and the effect of water level on microbial community was more effective in Lake Eymir. However, in both lakes, annual and seasonal changes and the actual biomasses, however, appeared to be mainly controlled by zooplankton grazing pressure and change in zooplankton composition.

### 4.3. Eymir mesocosms experiment

The key findings of the study as follows:
(i) Strong effects of water level on microbial communities via nutrients and submerged macrophyte growth were observed:

- Higher TN and TP concentrations in the shallow mesocosms and higher bacteria biomass.
- High abundance of macrophytes only in the shallow mesocosms and macrophytes affect the structure and functioning of the microbial communities by positively maintaining area for bacterial growth, negatively maintaining refuge for cladocerans and increasing cladoceran grazing on microbial community and allelopathic effect on bacteria

(ii) Strong effects of fish on both bottom up and top down control of microbial and plankton communities were observed

- Higher TN and TP concentrations in fish mesocosms and higher bacteria biomass, the effects being most notable in the shallow mesocosms,
- Fish-mediated trophic cascades on microbial community by altering the grazing pressure on microbial community.

RM-A results revealed that water level had a significant effect on TP and TN concentrations, the effect being stronger in the shallow mesocosms (Bucak et al., 2012). Higher concentrations can be attributed to enhanced nutrients concentration in the water due to evaporation (Özen *et al.*, 2010; Bucak et al., 2012). Overall bacteria, HNF and ciliate biomasses were higher in shallow mesocosms and these results support the fact that higher microbial biomass in eutrophic shallow lakes (Burns & Schallenberg, 2001; Muylaert *et a*l., 2003; Auer *et al*., 2004).

TP concentrations were higher in shallow mesocosms (Bucak et al. 2012) and bacteria: phytoplankton ratio was lower than that of the deep mesocosms where the TP concentrations were lower. The phytoplankton biomass was higher than bacteria biomass in shallow mesocosms and these results also support the idea that increase in bacterial abundance is slower than phytoplankton abundance with increasing nutrient concentrations (Cotner & Biddanda, 2002) due to increased protozoan grazing (Sanders *et al.,* 1992) and increased viral mortality (Weinbauer *et al.,* 1993). These results were coinsidence with the findings of some Mediterrenean shallow lakes (Conty *et al.,* 2007). They found that bacteria: chlorophyll-a ratio decreases with the increasing nutrient loading.

Water level had also indirect affect on microbial community via macrophyte devolopment. High macrophyte density only devoloped in shallow mesocosms and it shows that water level had strong effects on macrophyte growth (Bucak et al. 2012). These findings supports the idea that submerged plants may increase in the Mediterranean region due to changes in water levels which will occur due to climate change (Coops et al, 2003; Beklioglu et al. 2006).

There are limited studies on the interactions between submerged macrophytes and microbial plankton (Komarkova´ & Komarek, 1975; Kleppel *et al.,* 1980; Middelboe *et al.,* 1998; Mitamura & Tachibana, 1999; Reitner *et al.,* 1999; Scheffer, 1999; Theil-Nielsen & Søndergaard, 1999; Muylaert *et al.,* 2003). The PVI% increased in low water mesocosms following the water level decline in July. In the meantime, the bacterial biomasses were decreased in low water mesocosms in August and lower than high water mesocosms where PVI% was almost zero. These results support the idea that allelopathic effect of the macrophytes negatively affects the bacterial production (Stanley *et al.,* 2003).

In accordance with the study of Zingel and Nöges (2008) which showed that "The microbial loop was weaker in macrophyte dominated lakes", we found that the

contribution of microbes to plankton community suddenly decreased in August due to increased in macrophyte growth in both shallow fishless and shallow fish mesocosms. However, the decrease was more dramatic in shallow fish mesocosms due to sudden increase in total zooplankton biomass since increasing macrophyte provided protection from fish predation (Timms & Moss, 1984; Stansfield et al., 1997; Burks et al., 2002).

When we compared the bacteria biomasses in shallow and deep mesocosms in the the overall study period, the bacteria biomasses were higher shallow mesocosms where the macrophyte densities were higher. This results supports the idea that "The aquatic plants play an important role in the location of the greatest bacterial growth in the water column" (Wetzel & Søndergaard 1998; Nielsen & Søndergaard,1999; Wilcock *et al.,* 1999; Stanley *et al.,* 2003).

Mechanisms operating on zooplankton in macrophyte beds are also indirectly acting on protozoan community. Since submerged plants are refuge for cladocerans they had a negative effect on bacteria and HNF. In accordance with these findings, Cladoceran biomass increased and bacteria and HNF biomasses decreased in shallow fish mesocosms following an increase in macrophyte coverage The plants provided protection from fish predation (Burks *et al,* 2002).

A study of Jurgens and Jeppesen, (2000) which showed that when there was limited macrophytes growth, ciliate density were higher than that of high macrophyte growth, in accordance with this, ciliate biomass was decreased in shallow fish mesocosms in August and September due to increasing in PVI%. This may be related with increasing cladoceran grazing due to increasing PVI% since macrophyte provided protection from fish predation (Burks *et al,* 2002).

Mieczan (2008 and 2010) found that "The abundance and biomass of ciliates were significantly higher at sites with structurally most complex plants than in the open

water or sparsely vegetated sites and the results of this study demonstrate that ciliates probably use macrophyte vegetation as potential refuge". In accordance with these results, ciliate biomass increased in shallow fishless mesocosms due to increase in PVI% in August and September.

However, water level also had an impact on the cascading effects of the fish which was higher in the shallow mesocosm, in accordance with field observations (Jeppesen *et. al.,* 1997) and attributed to a higher fish density and biomass per unit of volume in shallow lakes (Jeppesen *et al.,* 1997). The effect of fish on both classical food web and microbial loop together was not fully explored studied (Christoffersen *et al.,* 1993; Takamura *et al.,* 1995; Özen et al. in press). RM-A results revealed that fish had a significant effect on TP and TN concentrations, the effect being stronger in the shallow mesocosms with fish (Bucak et al. 2012). RM-A results showed that fish had a significant positive effect on phytoplankton biomass and negative effect on zooplankton: phytoplankton ratio as it observed in the study of Nishimura *et al* (2011). Higher phytoplankton biomass leads to higher TP and TN in fish mesocosms (Søndergaard *et al.,* 2008). Thus, higher concentrations can be attributed to fish mediated nutrient excretion and regeneration of nutrients and resuspension of settled phytoplankton cells and detritus (Breukelaar *et al.,* 1994; Vanni *et al.,* 1997; Vanni 2002; Roozen *et al,.* 2007). As a result of higher nutrient concentrations, higher bacteria biomasses were observed in both shallow and deep fish mesocosms.

RM-A results also revealed that fish had significant negative affect on bacteria: phytoplankton ratio. This may be related with decreasing phytoplankton exudation due to decreasing zooplankton grazing and less organic carbon was available for bacteria growth (Gasol & Duarte, 2000). In accordance with the Zingel and Nöges (2008) who claimed that the microbial community was relatively stronger in phytoplankton dominated lakes, we found that overall contribution of microbial community was higher in phytoplankton dominated deep mesocosms. This can be explained the fact that to a large extent, microbial community (bacteria, HNF and ciliates) depend directly or indirectly on phytoplankton as a food source.

Exudates produced by phytoplankton are an important substrate for aquatic bacteria in shallow lakes (e.g. Kamjunke *et al.,* 1997). HNF and ciliates feed on bacteria (e.g. Sanders *et al.,* 1989) and small phytoplankton (e.g. Weisse 1990). Therefore, microbial community was relatively stronger in phytoplankton dominated lakes (Zingel & Nöges, 2008).

Although the top down effect of zooplankton on the microbial loop was well studied (Jürgens *et al.,* 1994, Jürgens & Jeppesen, 1998; Wickam, 1998; Zöllner *et al.,* 2003, 2009), relatively little is known about the impacts of fish-mediated trophic cascades on microbial loop processes (Riemann, 1985; Pace & Funke, 1991; Pace & Cole; 1996).

RM-A results revealed that fish had a significant negative affect on the biomasses of zooplankton, cladocerans, copepods, contribution of zooplankton to plankton community and zooplankton: phytoplankton ratio. This results showed the strong cascading effects of fish as demonstrated elsewhere (Carpenter *et al.,* 1987).
Strong grazing effect of fish on zooplankton resulting in lower biomass of copepods and cladocerans, being particularly low in shallow fish mesocosms as expected (Brooks & Dodson, 1965). There was a change in composition of zooplankton due to the presence of planktivorous fish as expected (Riemann, 1985; Christoffersen *et al.,* 1993; Jeppesen *et al.,* 1996). A shift occurred from dominance of calanoid copepods and *Daphnia* to small-sized zooplankton such as *Chydorus* spp., *Alona* spp. and nauplii in fish mesocosms. This, in turn, affected bacterial biomass and production (Markosova and Jezek, 1993; Riemann, 1985) by altering the grazing pressure on bacteria. Thus, overall bacterial biomasses were higher in both shallow and deep fish mesocosms during the study period. Zooplankton: ciliate ratio was lower in fish mesocosms and as a result of this ciliate: HNF ratios were higher in both shallow and deep fish mesocosms. As a result of decreasing grazing pressure of HNF on bacteria, bacteria biomasses were higher in both shallow and deep fish mesocosms (Jurgens *et al*., 2000; Kisand *et al.,* 2000; Simek *et al*., 2000).

In a study of Christoffersen *et al*., (1993) showed that the presence planktivorous fish changed the biomass and composition of zooplankton in eutrophic lake and this is in turn affected microbial loop. When cladoceran dominated they controlled the biomass of phytoplankton, HNF, rotifers and bacteria. However, when fish reduced the cladoceran community microbial community developed with high HNF biomass. In accordance with these findings, cladocera: bacteria, cladocera: HNF, cladocera: phytoplankton ratios were higher in both shallow and deep fishless mesocosms.

Copepod biomasses were higher in both shallow and deep fishless mesocosms. Higher ciliate biomasses in both shallow and deep fish mesocosms and higher HNF biomasses in both shallow and deep fishless mesocosms were observed. These results can be explained with the fact that Copepods grazed on ciliates and decreased the grazing pressure of ciliates on HNF (Sommer et al., 2003).

Higher ciliate: HNF and lower zooplankton: ciliate, cladocera:ciliates and copepods:ciliate ratios in shallow fish mesocosms ratios support the idea that there would be more strong bottom up control and less top down control in Mediterranean lakes in the future (Conty *et al*., 2007).

To sum up, both water level and fish strong impact on nutrients and this in turn change the microbial biomass. Water level had also significant impact on macrophyte growth. As a consequence of submerged plant devolopment, changes in the biomasses of microbial communities were observed. Fish had also impact the microbial community through changing the trophic cascade on microbial community. Water level had a significant effect on bacteria biomass. Fish had a significant effect on ciliate biomass.Water level and fish interaction had significant effect on HNF. In conclusion, water level and fish interaction had a significant effect on total microbial community biomass.

### 4.4. Climate change and microbial loop

#### 4.4.1 Long-term effects of warming and nutrients on microbes and other plankton in mesocosms

As foreseen, major seasonal changes occurred in microbial and other planktonic biomasses from the ice-covered period (February to March) to the ice-free period (mid-March to May), with many-fold increases in most variables in all treatments accompanied by an increase in TP and a decrease in orthophosphate, nitrate and TN as are typical for shallow lakes during this season (Søndergaard *et al*., 2005).

We found that warming had a smaller effect than nutrients on the biomass of the microbial community and that warming and nutrients combined exhibited complex interactions as in the previous study by Christoffersen *et al*. (2006). Mesocosm warming experiments, in England involving nutrient enrichment also showed nutrients to have a far greater impact than temperature on the plankton food web, zooplankton and phytoplankton (McKee *et al*., 2002, 2003; Moss *et al*., 2003; Feuchtmayr *et al*., 2007).

We did not find a direct effect of warming on the biomass of bacteria or ciliates, although warming significantly added to the positive effect of nutrients on these organisms. A similar observation was made for HNF in a previously published study of the mesocosms (Christoffersen *et al*., 2006). No warming effect was revealed for chlorophyll-*a* and the zooplankton groups analysed, whereas chlorophyll-*a* and total zooplankton biomass as expected were higher in nutrient-enriched mesocosms. The contribution of rotifers to total zooplankton biomass was higher at the highest nutrient level, while the contribution of copepods was lower. These nutrient effects were in accordance with other studies (Mathes & Arndt, 1994; Jeppesen *et al.*, 2000; Burns & Galbraith, 2007). The contribution of phytoplankton to total plankton biomass increased with rising nutrient concentrations and the contribution of microbial biomass decreased as observed in other studies of eutrophication (Mathes & Arndt, 1994).

Our results revealed the indications of synergistic effects of nutrients and warming on food web dynamics as judged from changes in selected ratios. For example, the lowest zooplankton: phytoplankton biomass ratio occurred in the warm nutrient-rich (H+NP) mesocosms. It is well established that this ratio decreases with increasing eutrophication (e.g. Jeppesen *et al*., 2000, 2003), but our results indicate that the effect will be stronger when lakes get warmer. This may be attributed to higher fish predation on zooplankton in warm systems, resulting in lower grazing control of phytoplankton (Jeppesen *et al*., 2009, 2010). At high fish predation in warm lakes the zooplankton is dominated by small-bodied species (Meerhoff *et al*., 2007; Havens *et al.*, 2011; Iglesias *et al.*, 2011), and the abundance of rotifers (not observed in our study), ciliates (Crismann & Beaver, 1990; Havens *et al.*, 2011) and HNF tend to be higher, as in our study.

The bacterial biomass is distinctly affected by grazing (Pace *et al*., 1990), and heterotrophic flagellates tend to be the major bacterivore in fresh waters, followed by ciliates, rotifers and cladocerans (Jürgens & Jeppesen, 2000; Zöllner *et al*., 2003). However, rotifer grazing on bacteria may sometimes be far more important than that of protozoans (Starkweather, Gilbert & Frost 1979; Bogdan, Gilbert & Starkweather, 1980; Boon & Shiel, 1990; Arndt, 1993). We found the highest HNF: bacteria biomass ratio as well as the highest Rotifera: bacteria biomass ratios in the warm nutrient-rich mesocosms (H+NP), which indicates high predation on bacteria. Rotifers have been found to be more important grazers of bacteria in the nutrient-rich warm lakes (Conty, Garcia-Criado & Becares, 2007), likely as a result of higher fish predation on large-bodied zooplankton in such warm lakes (Gyllström *et al*., 2005). Thus, the bacteria: phytoplankton ratio was lowest in the nutrient-rich warm mesocosms, also suggesting grazer control of bacterial biomass. Several studies have demonstrated the bacteria: phytoplankton ratio to be lowest in eutrophic lakes where the importance of microzooplankton and protozoans are highest (Auer, Elzer & Arndt, 2004; Biddanda, Ogdahl & Cotner, 2001; Cotner & Biddanda, 2002).

Higher grazer control of bacterial biomass in warm mesocosms may also explain why bacterial production, contrary to our expectations, did not increase with warming, but was affected only by nutrient addition. In accordance with our results, Roland *et al.* (2010) found the ratio of bacteria to phytoplankton abundance (Chl-*a*) to be lower in tropical than in temperate lakes, which they attributed to dominance of microzooplankton and protozoans in tropical lakes.

Christoffersen *et al*. (2006) found higher biomasses of bacteria and HNF in late spring and summer (April-September) than in autumn and winter (October-March). Likewise, we found higher biomasses of bacteria and HNF in the ice-free period (April and May) than in the ice-covered period (February and March), but only HNF biomass was lower in ice-free period in the warm mesocosms at high nutrient levels (H+NP). This might be due to higher ciliate grazing in these mesocosms. With the expected decrease in ice cover in the future in north temperate lakes, the importance of the microbial community may therefore decline relative to phytoplankton (and fish), particularly in systems with high nutrient levels.

Although the results of the study by Christoffersen *et al*. (2006) were partly in accordance with ours in emphasizing the stronger effect of nutrients compared to temperature, there were also some differences between two studies. As in our study, Christoffersen *et al*. (2006) found that "Warming by itself to have no effect on the abundance of bacteria and HNF. They showed, however, that warming significantly modified the positive effect of the nutrients and that only at ambient temperatures did the whole microbial assemblage respond positively to nutrients". By contrast, we found positive warming-nutrient interactions in the microbial community. Whether these differences reflect that the mesocosms have been running for a longer time is uncertain as the nitrogen loading and fish abundance also have changed in the meantime. We believe, however, that our study was run under more realistic conditions, as the mesocosms were severely nitrogen-limited during the early phase of the experiment (2003-04), and because allowing fish breeding (since 2006) led to more natural fish densities and size variation than during the previous investigation.

Furthermore, after seven years the mesocosms have passed the early transient phase that typically characterises such experimental systems. The results of our study strongly support that nutrient and warming together have a stronger effect on the pelagic communities than either of them alone. In conclusion, we found that when warming and nutrient enrichment act in combination, the microbial food web structure is affected more notably than when warming and nutrient enrichment act alone. Consequently, the effects of warming may be strongest in nutrient-enriched systems. Warming may strengthen eutrophication (Jeppesen *et al.*, 2009, 2011) and by that further stimulate changes in the microbial as well as the classical aquatic food web and their interactions.

# CHAPTER 5

# CONCLUSION

## 5.1 Bottom Up Control

Nutrients as a bottom-up control had a significant effect on the biomass of the microbial community in studied lakes and mesocosms.

Both field study results and mesocosms experiment results showed that:

- Higher phosphorous concentrations increase the bacterial production (Nelson & Carlson, 2008).
- Primary production increass with N availability (Faithfull *et al*., 2011).
- Nutrient enrichment led to increasing in abundance and biomass of all components of the pelagic food web (Pace, 1986; Berninger *et al.,* 1991) and microbial community Burns & Schallenberg, 2001; Muylaert *et al*., 2003; Auer *et al*., 2004). Therefore, nutrient supply influenced the structure of the pelagic community and had an effect on the interactions among the community components.
- The contribution of phytoplankton to total plankton biomass increased with rising nutrient concentrations and the contribution of microbial biomass decreased as observed in other studies of eutrophication (Mathes & Arndt, 1994; Auer, Elzer & Arndt, 2004; Biddanda, Ogdahl & Cotner, 2001; Cotner & Biddanda, 2002). Our results were in accordance with other studies that report higher proportions of microbes in lakes with lower nutrient availability

(Hwang & Heath, 1997, Fahnenstiel *et al.,* 1998, Biddanda *et al.,* 2001, Cotner & Biddanda, 2002) and decreasing importance of the microbial food web with increasing productivity of the system (Porter *et al.,* 1988; Weisse, 1991, Azam & Smith, 1991, Biddanda & Cotner, 2001).

- Results from lakes and mesocosms showed that competition for nutrients may be a critical aspect of bacteria-phytoplankton interactions (Cotner, 1992; Elser and George, 1995; Brett *et al*., 1999) and both bacteria and phytoplankton biomasses were regulated by zooplankton (Cyr & Pace, 1992; Jürgens, 1994; Jürgens & Jeppesen, 2000).

### 5.2 Top Down Control

Field study and mesocosms experiment results support the previous findings that HNF were mainly responsible for bacterial biomass control (Fenchel 1982; Giide 1986; Pernthaler *et al.,* 1996; Sanders *et al.,* 2000; Callieri *et al.,* 2002) and ciliates strongly grazed on HNF (Sanders *et al.,* 1989, Simek *et al.,* 1990; Weisse *et al.,* 1990; Sherr *et al.,* 1991; Kivi & Setela, 1995; Szelag-Wasielewska & Fyda 1999; Premke & Arndt, 2000; Zingel *et al*., 2007).

Our results from field sampling, in situ grazing experiment and mesocosms experiments revealed that the different zooplankton composition had different cascading effect on microbial community members:

- Cladocera grazed on bacteria (Jürgens,1994; Kamjunke *et al*., 1999), HNF (Wickham,1993), ciliates (Jurgens, Arndt & Zimmermann, 1997; Marchessault & Mazumder, 1997), Daphnids grazed on all microbial community (Müller *et al.,* 1991, Weisse, 1991; Carrick *et al.,* 1991; Christoffersen *et al.,* 1993; Burn & Schallenberg, 1996; Modenutti *et al.,* 2003).
- Clanoid copepods on ciliates (Burns and Gilbert, 1993; Wiackowski et al., 1994; Wickham, 1995).

- Cyclopoid copepods on HNF (Sommer *et al.*, 2003), ciliates Burns & Gilbert, 1993; Wiackowski *et al*., 1994; Wickham, 1995).
- Rotifera on bacteria (Starkweather, Gilbert & Frost 1979; Bogdan, Gilbert & Starkweather, 1980; Boon & Shiel, 1990; Arndt, 1993; Conty, Garcia-Criado & Becares, 2007). HNF (Pernthaler *et al.,* 1996; Tadonleke *et al.,* 2004) and ciliates (Gilbert, 1980; Arndt, 1993; Gilbert & Jack, 1993, Sommer *et al.,* 2003).

Our results support the idea that weak or no coupling of HNF and bacteria under eutrophic conditions compared to oligotrophic systems (Gasol & Vaque, 1993; Tzaras & Pick, 1994; Wieltschnig *et al*., 2001). However, we found that top-down control of cladocerans on microbial loop and ciliate on HNF decreased with increasing nutrients in snap shot sampling lakes and Lakes Mogan and Eymir and mesocosms experiments.

Field and mesocosms results revealed that the contribution of rotifers to total zooplankton biomass was higher at the highest nutrient level, while the contribution of copepods and cladocera were lower. These nutrient effects were in accordance with other studies (Mathes & Arndt, 1994; Jeppesen *et al*., 2000; Burns & Galbraith, 2007).

### 5.3 Submerged plants

Submerged plant may also be another indirect mechanism that may affect microbial community (Wetzel & Søndergaard, 1998; Wilcock *et al.,* 1999; Stanley *et al.,* 2003). Snap shot sampling and seasonal monitoring results showed that presence and absence of submerge plant might cause the indifference between pelagic and littoral zones of microbial and zooplankton communities of studied lakes (Wu *et al.,* 2007) since plant density may influence the ecology and water biochemistry of lakes (Chambers *et al.,* 2008), offer a shelter from predators to many organisms such as young fish and zooplankton (Scheffer, 1998; Nurminen *et al.,* 2007), serve food

source for phytoplankton and bacteria (Kuczyńska-Kippen, 2005; Vieira *et al.,* 2007; Tessier *et al.,* 2008).

Snap shot sampling and seasonal monitoring results also supported the idea that allelopathic effect of plants had a negative effect on bacterial production (Stanley *et al.*, 2003).

### 5.4 Fish

Snap shot sampling, seasonal monitoring and Eymir mesocosms experiment showed that the impacts of fish-mediated trophic cascades effect on microbial loop community (Riemann, 1985; Pace & Funke,1991; Pace & Cole; 1996).

More abundant plankti-benthivorous fish in studied lakes and mesocosms might enhance predatory control of zooplankton (Jeppesen *et al*., 2009, 2010) especially on the biomasses of cladocerans and copepods (Brooks & Dodson, 1965 Gliwicz, 2003; Jeppesen *et al.,* 2008; Schulze, 2011) with cascading effects on bacteria, and protozoans (Porter & McDonough, 1984; Nõges *et al*., 1998; Jürgens & Jeppesen, 2000).

Eymir mesocosms experiments results also revealed that fish had a significant effect on TP and TN concentrations. Higher phytoplankton biomass with higher fish biomass leads to higher TP and TN concentrations which can be attributed to fish mediated nutrient excretion and regeneration of nutrients and resuspension of settled phytoplankton cells and detritus (Breukelaar *et al*., 1994; Vanni *et al.,* 1997; Vanni 2002; Roozen *et al,*. 2007). Higher nutrient concentrations were resulted with higher bacteria biomasses in both shallow and deep fish mesocosms.

## 5.5 Global warming

Global warming is another factor that may affect both classical food web and microbial communities Climate models also predict that precipitation and accordingly nutrient loading to lakes (eutrophication) will increase in Northern Europe, warmer and drier conditions, decrease and change in precipitation will be observed in Mediterranean zone (Giorgi, 2006; Giorgi & Lionello,2008; .Paz *et al*., 2010).

Our results from Lemming mesocosms showed that warming had a smaller effect than nutrients on the biomass of the microbial community and that warming and nutrients combined exhibited complex interactions as in the previous study by Christoffersen et al. (2006). We did not find a direct effect of warming on the biomass of bacteria or ciliates, although warming significantly added to the positive effect of nutrients on these organisms but we found the positive direct effect of warming on HNF. However snap shot sampling results showed that temperature had a significant effect on bacteria and HNF. The results of our Lemming mesocosms study strongly support that nutrient and warming together have a stronger effect on the pelagic communities than either of them alone. In conclusion, we found that when warming and nutrient enrichment act in combination, the microbial food web structure is affected more notably than when warming and nutrient enrichment act alone.

Water level fluctuations via global warming may affect microbial communities. Eymir mesocosms experiments results showed that strong effects of water level on microbial communities via nutrients and submerged macrophyte growth were observed:

- Higher TN and TP concentrations in the shallow mesocosms and higher bacteria biomass.

- Water level affected macrophyte growh and macrophytes affected the structure and functioning of the microbial communities by positively maintaining area for bacterial growth, negatively maintaining refuge for cladocerans and increasing cladoceran grazing on microbial community and allelopathic effect on bacteria.

### 5.6 Seasonality

Seasonal monitoring results and Lemming mesocosms experiment results showed that annual and seasonal changes and the actual biomasses of microbial food web (Jurgens et al., 2000; Muylaert *et al.* 2002) and phytoplankton (Christoffersen et al., 1993) appeared to be mainly controlled by zooplankton grazing pressure and change in zooplankton composition in Lakes Mogan and Eymir and Lemming mesocosms as it discussed separately in the text before.

### 5.7 Conclusion

Our results from both field studies and mesocosms experiments strongly support that both top down and bottom up factors have a robust effect on the microbial and plankton food web. The different response of microbial loop community to increasing nutrient levels may be explained by changing top down control within microbial loop (Rae & Vincent 1998; Christoffersen *et al.,* 2006), the direct and indirect impact of different zooplankton groups on microbial loop (Porter & McDonough, 1984; Nõges *et al.,* 1998; Jürgens & Jeppesen, 2000).

In addition, results from Lakes Mogan and Eymir revealed that seasonality was also an important factor for determining the role of top down and bottom up factors on microbial and plankton communities. Eymir mesocosms experiment showed that water level changes might effect microbial community via nutrients and macrophyte growth.

Global warming may also be another important factor for determining the role of microbial communities in the ecology of shallow lakes. The differences for total nitrogen and temperature between Turkish lakes showed that global warming may also effect the relation between top down and bottom up factors via increasing warming and eutrophication. However, results of mesocosms experiment in Denmark revealed that when warming and nutrient enrichment act in combination, the microbial food web structure is affected more notably than when warming and nutrient enrichment act alone and the effects of warming may be strongest in nutrient-enriched systems. Consequently, the effects of warming may be strongest in our region in the future. Warming may exacerbates eutrophication (Özen *et al.*, 2010; Jeppesen *et al.*, 2009, 2011) and in a consequence of that further stimulate changes may occur in the microbial as well as the classical aquatic food web and their interactions.

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- M.Sc., Middle East Technical University, Department of Biology,2006.
- B.S, Hacettepe University, Department Of Biology, 2002.
- High School, Eskişehir Yunus Emre, 1998.

### WORK EXPERIENCE

| Year | Enrollment | University | Department |
|---|---|---|---|
| 2004- 2012 | Research Assistant | METU | Biology |
| January 2010 – May 2010 | Quest researcher | NERI-Denmark | Limnology |

### TEACHING EXPERIENCE

- "Freshwater Ecology Laboratory" Assistantship
- "Introduction to Biometry Laboratory" Assistantship
- "Biometry Laboratory" Assistantship
- "Microbiology Laboratory" Assistantship
- "Applied Ecology" Assistantship
- "Ecology" Assistantship
- "General Biology Laboratory" Assistantship

## PUBLICATIONS AND PROJECTS

### Publications:

### İnternational Publications (SCI Journals)

1. Erik Jeppesen, Brian Kronvang, Mariana Meerhoff, Martin Søndergaard, Kristina M. Hansen, Hans E. Andersen, Torben L. Lauridsen, Meryem Beklioglu, **Arda Özen** & Jørgen E. Olesen. (2009). Climate change effects on runoff, catchment phosphorus loading and lake ecological state, and potential adaptations. **Journal of Environmental Quality,** 38: 1930- 1941.

2.**Arda Özen**, Burcu Karapinar, Ismail Küçük, Erik Jeppesen, Meryem Beklioglu. (2010). Drought-induced changes in nutrient concentrations and retention in two shallow Mediterranean lakes subjected to different degrees of management. **Hydrobiologia**, 646: 61-72.

3.Erik Jeppesen, Brian Kronvang, Jørgen E. Olesen, Joachim Audet, Martin Søndergaard, Carl C. Hoffmann, Hans E. Andersen, Torben L. Lauridsen, Lone Liboriussen, Meryem Beklioglu, Mariana Meerhoff, **Arda Özen** & Korhan Özkan,(2011). Climate change effects on nitrogen loading from cultivated catchments: implications for nitrogen retention, ecological state of lakes and adaptation. **Hydrobiologia**,663:1-21.

4. **Arda Özen**, Michal Sorf, Carolina Trochine, Lone Liboriussen, Meryem Beklioglu, Martin Søndergaard, Torben l. Lauridsen, Liselotte Sander Johansson & Erik Jeppesen (2012) Temperature and nutrient effects on freshwater microbial and planktonic communities in climate warming experimental ponds after seven years of incubation. **Freshwater Biology** doi:10.1111/j.1365-2427.2012.02824.x.

**Oral Presentations & Proceedings in International Conferences**

1. **Özen A.** B. Karapinar Ç. B. Muluk Ö. Karabulut & M. Beklioglu. Shift to turbid water state with loss of submerged plants five years after biomanipulation in Lake Eymir, Turkey 29. "Shallow Lakes in a changing world" the 5th international Symposium on the Ecology and Management of Shallow Lakes 5 - 9 June, 2005 in Dalfsen, the Netherlands (poster).

2. Meryem Beklioglu & **Arda Özen**: 2007. Drought-induces changes in macrophytes, nutirent and major ions in Turkish shallow Lakes. 5th Symposium for European Freshwater Sciences (SEFS5), Palermo, Italya,Temmuz 8-13, 2007 (oral presentation).

3. **Özen, Arda**; Karapinar, Burcu; Kucuk, Ismail; Jeppesen, Erik; Beklioğlu, Meryem. Drought-Controlled Nutrient Mass Balances in a System of Two Mediterranean Shallow Lakes, Turkey. SHALLOW LAKES CONFERENCE 'Structure and Function of Shallow lakes' URUGUAY 2008 (oral Presentation).

4.Jeppesen, Erik; Sondergaard, Martin; Meerhoff, Mariana; Liboriussen, Lone; Lauridsen, Torben; Landkildehus, Frank; Beklioglu, Meryem; Kronvang, Brian; Amsinck, Susanne; Özen**, Arda**. Relative importance of temperature and nutrient gradients in shallow lake functioning: empirical and experimental evidence. SHALLOW LAKES CONFERENCE 'Structure and Function of Shallow lakes' URUGUAY 2008 (oral Presentation).

5.Tavşanoğlu, Nihan; **Özen, Arda**; Jeppesen, Erik; Beklioğlu, Meryem.Diel horizontal and vertical distribution of zooplankton and the refuge effect of macrophyte in warm-climate Turkish lakes.SHALLOW LAKES CONFERENCE 'Structure and Function of Shallow lakes' URUGUAY 2008 (oral Presentation).

6.Beklioğlu, Meryem; Özen**, Arda**; Çakıroğlu, Idil; Tavşanoğlu, Nihan; Oğuzkurt, Didem; Özkan, Korhan; Levi, Eti; Jeppesen, Erik. Role of nutrients and climate on functioning of the Turkish Shallow lakes using space for time substitute approach. SHALLOW LAKES CONFERENCE 'Structure and Function of Shallow lakes' URUGUAY 2008 (oral Presentation).

7.M. Beklioglu, A. İdil Çakıroglu, E. Levi, N. Tavşanoğlu, **Arda Özen**, E. Jeppesen, Susanne Lildal Amsinck, K. Özkan, Lisa Doner. Past to present and to future: Ecology of Turkish Shallow lakes. International Paleoclimatology Workshop, 20-23 October, 2008, Van, Turkey (invited talk)

8.M. Beklioglu, **A. Özen**, O. Kerimoğlu. Impact of hydrology of Turkish lakes, nutrients, salinity and biodiversity. International Workshop on Impact of Climate change Aquatic ecosystems and Society, 28-29 June,2008, METU, Ankara, Turkey.

9.Meryem Beklioglu, Nihan Tavşanoglu, İdil Çakıroglu, **Arda Özen**, Eti Levi, Korhan Özkan, Didem Oguzkurt, Mengü Türk, Tuğba Bucak, Erik Jeppesen. Role of nutrients and climate on functioning of the Turkish shallow lakes. SEFS6, Symposium of European Freshwater Sciences 6, 17-21 August, 2009, Sinaia, Romenia.

10.Erik Jeppesen, Brian Kronvang, Mariana Meerhoff, Martin Søndergaard, Kristina M. Hansen, Hans E. Andersen, Torben L. Lauridsen, Meryem Beklioglu, **Arda Ozen** & Jørgen E. Olesen. 2009.Shallow lake dynamics in a climate change perspective, SEFS6, Symposium of European Freshwater Sciences 6, 17-21 August, 2009, Sinaia, Romenia.

11.Ü. Nihan Tavşanoğlu, A. İdil Çakıroğlu, Eti E. Levi, **Arda Özen**, Korhan Özkan, Didem Oğuzkurt, Tuba Bucak, Gizem Bezirci, Erik Jeppesen & Meryem Beklioğlu. Non-native Fish Species in 30 Shallow Lakes Located from North to South of Turkey. New approaches for assessing the impacts of non-native freshwater fishes in the Mediterranean region. Workshop. 6–29 October 2010 in Muğla, Turkey.

**Presentations in National Meeting (abstract published)**

1. Arda Özen & Meryem Beklioğlu 2007 Otrofik Eymir Gölünün Biyomanipulasyon ile Restorasyonunda Kuraklık Etkisi. 7. Ulusal Çevre Mühendisliği kongresi 24-27 Ekim, İzmir. Yaşam Çevre ve Teknoloji Bildiriler Kitabı, sayfa 282-291. Emre Basımevi,İzmir.

**2.** Meryem Beklioglu & Arda Özen. 2007. Hidroloji Besin Tuzları ve Balık Stokunun Küresel ısınma ile BirlikteTürkiye'deki Sığ göllerin Ekolojisine Etkileri. 7. Ulusal Çevre Mühendisliği kongresi 24-27 Ekim, İzmir. Yaşam Çevre ve Teknoloji Bildiriler Kitabı, sayfa 403-412. Emre Basımevi, İzmir.

**3.** Meryem Beklioglu & Arda Özen. 2007. Ulkemiz sıg gollerinde kuraklık etkisi ve ekolojik tepkiler. Uluslararası Kuresel Iklım Degisikligi ve Cevresel Etkiler Konferansı Bildiriler kitabı. Sayfa 299-306.

**4.** Meryem Beklioğlu, Arda Özen, Ayşe İdil Çakıroğlu, Didem Oğuzkurt, Korhan Özkan, Nihan Tavşanoğlu, Eti Levi, Mengü Türk.2008. Ülkemiz Sığ Göllerin Ekolojik Yapısında Ötrofikasyon ve İklim Değişiminin Olası Rolleri. 3.Ulusal Limnoloji Sempozyumu, İzmir.

**5.** Meryem Beklioğlu, Ayşe İdil Çakıroğlu, Korhan Özkan, Didem Oğuzkurt, Lisa Doner, Arda Özen, Ceran Şekeryapan, Yetkin Alıcı, Erik Jeppesen.2008. Sığ ve Derin Göllerde Besin Ağının Karbon ve Azot Kalıcı İzotopları Kullanarak Belirlenmesi. 3.Ulusal Limnoloji Sempozyumu.

**6.** Arda Özen, Burcu Karapınar, İsmail Küçük, Erik Jeppesen & Meryem Beklioğlu.Akdeniz İklim Bölgesinde Aynı Havzada Yeralan Mogan ve Eymir Göllerinde Kuraklığın Besin Tuzu Bütçelerine Olan Etkisi..62. Türkiye Jeoloji Kurultayı, 13-17 Nisan,2009 Ankara-Türkiye.

**7. Arda ÖZEN**, Michal Sorf, Carolina Trochine, Lone Liboriussen, Meryem Beklioglu, Martin Søndergaard, Torben L. Lauridsen, Liselotte Sander Johansson, Erik Jeppesen. Sıcaklık ve Besin Tuzlarının Mikrobik ve Planktonik Komüniteler Üzerindeki Uzun Dönemli Etkileri: Mezokozm Deneyi. 5. Limnoloji Sempozyumu, 27-29 Ağustos 2012 Isparta-Türkiye.

8. **Arda Özen**, Nihan Tavşanoğlu, Ayşe İdil Çakıroğlu, Eti Levi, Gizem Bezirci, Erik Jeppesen, Meryem Beklioğlu. Besin Tuzları, Avlanma Baskısı ve Küresel Isınmanın Ülkemizdeki Bazı Sığ Göllerdeki Mikrobik Çevrim Üzerindeki Etkileri. 5. Limnoloji Sempozyumu, 27-29 Ağustos 2012 Isparta-Türkiye.

9. Ü.Nihan Tavşanoğlu, A.İdil Çakıroğlu, E.Ester Levi, **Arda Özen**, Tuba Bucak, Gizem Bezirci, Didem Oğuzkurt, Korhan Özkan, Erik Jeppesen, Meryem Beklioğlu. İklim Değişiminin Sığ Göllerin Yapı ve İşlevleri Üzerindeki Etkileri: Zaman Yerine Mekân Yaklaşımı. 5. Limnoloji Sempozyumu, 27-29 Ağustos 2012 Isparta-Türkiye.

10. Nur Filiz, A. İdil Çakıroğlu, Ü. Nihan Tavşanoğlu, Şeyda Erdoğan, Tuba Bucak, E.Ester Levi, **Arda Özen,** Gizem Bezirci, Meryem Beklioğlu. Su Seviyesi ve Nutrient Değişikliklerinin Perifiton-Makroomurgasız Etkileşimleri Üzerine Etkisi: Mezokozm Deneyi. 5. Limnoloji Sempozyumu, 27-29 Ağustos 2012 Isparta-Türkiye.

11. Ü. Nihan Tavşanoğlu, A. İdil Çakıroğlu, Şeyda Erdoğan, Tuba Bucak, Nur Filiz, E.Ester Levi, **Arda Özen**, Gizem Bezirci, Meryem Beklioğlu. Küresel İklim Değişikliğinin Ötrofikasyon ve Hidroloji Etkileşimiyle Birlikte, Göl Ekosistem Yapı ve Dinamiklerine etkileri: Mezokozm Deneyi. 5. Limnoloji Sempozyumu, 27-29 Ağustos 2012 Isparta-Türkiye.

12. Tuba Bucak, A. İdil Çakıroğlu, Ü. Nihan Tavşanoğlu, Eti Ester Levi, Gizem Bezirci, Nur Filiz, Şeyda Erdoğan, **Arda Özen,** Deniz Önal, Jan Coppens, Meryem Beklioğlu. Beyşehir Gölü Havza Ölçekli Ekolojik İzleme. 5. Limnoloji Sempozyumu, 27-29 Ağustos 2012 Isparta-Türkiye.

**Book Chapters:**

Özen A. & M. Beklioglu Sulakalanlarla ilgili temel bilgiler, pp: 11-23. In Sulakalan yönetim planlaması rehberi, 176 pp Ankara, 2007.

**ACADEMIC RESEARCH PROJECTS**

**Institutional** (BAP,DPT)

- Ülkemiz Sığ Göl Sulakalanlarının ekolojik yapısının belirlenmesinde su seviyesi değişimi, besin tuzlarının yoğunluğu ve balık stokunun önemi BAP-08-11-DPT-2002-K120510 (2004-2006) 18.000 TL.
- "Sığ Göllerin Ekolojik Yapisinin Belirlenmesinde Mikrobik Çevrimin Rolü BAP-08-11-DPT-2002K120510 (2010) 6500 TL.

**National**

- Ülkemiz sığ göllerinin ekolojik yapisi, iklim ve insan kullanimi etkileşiminin bütünsel ve hassas yöntemlerle belirlenerek koruma ve iyileştirme stratejilerinin geliştirilmesi. TÜBİTAK, ÇAYDAĞ 105Y332. (2005-2008). 400.000 TL, (Principal investigator: Assistant Prof. Dr. Didem Oguzkurt).
- M. Beklioglu, İnfo-Biz-Çevre ve Orman Bakanlığı: Türkiye Çevresel Veri Değişim Ağının Kurulması için Modelleme ve izleme sistemi oluşturulması Destek Verilmesi Projesi – TEIEN. 2009-2010. (Principal investigator: Prof.Dr. Meryem Beklioğlu).
- "Sığ Göllerin Ekolojik Yapisinin Belirlenmesinde Mikrobik Çevrimin Rolü, TUBITAK CAYDAG 109Y181 (2010-2011). 25000 TL. (Principal investigator: Prof.Dr. Meryem Beklioğlu).

- Akdeniz İklim Kuşağındaki Sığ Göllerde Suiçi Bitkilerin Yapısal Rolü İle Gelişimini Etkileyen Faktörlerin Geçmişte, Günümüzde ve Daha Sıcak Isınan Koşullarda Belirlenerek Uyum ve Azaltma Stratejilerinin Oluşturulması TUBITAK CAYDAG 110Y125 (2011-2014).302269 TL. (Principal investigator: Prof.Dr. Meryem Beklioğlu).

**International**

- Greek – Turkish cooperation for the strengthening of protection and management of wetland areas (European Directive 2000/60). Start: 2004-2006, Supported by Greek Ministry of Foreign Affairs (34,000 EURO). (Principal investigator: Prof.Dr. Meryem Beklioğlu).
- Implications of climate-enforced temperature changes on freshwater microbial community studied in artificial ponds in Lemming Denmark 2010 (NERI-DENMARK), (Principal investigator: Erik Jeppesen).
- EU- FP7-ENV-2009-1: Collaborative project, REFRESH. Adaptive Strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems, WP3. Start Year: 2010 End Year:2014. (Principal investigator: Erik Jeppesen).