IMPACT OF WATER LEVEL FLUCTUATIONS AND FISH ON MACROINVERTEBRATE COMMUNITY AND PERIPHYTON GROWTH IN SHALLOW LAKES - A MESOCOSM APPROACH

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submitted by **ECE SARAOĞLU** in partial fulfillment of the requirements for the degree of **Master of Science in Biology Department, Middle East Technical University** by,

Prof. Dr. Canan Özgen
Dean, Graduate School of **Natural and Applied Sciences** _____

Prof. Dr. Musa Doğan
Head of Department, **Biology** _____

Prof. Dr. Meryem Beklioğlu Yerli
Supervisor, **Biology Department, METU** _____

Prof. Dr. Erik Jeppesen
Co-Supervisor, **Biology Department, Aarhus University** _____

Examining Committee Members:

Prof. Dr. Ayşen Yılmaz
Institute of Marine Sciences, METU _____

Prof. Dr. Meryem Beklioğlu Yerli
Biology Department, METU _____

Assoc. Prof. Dr. Can Bilgin
Biology Department, METU _____

Assoc. Prof. Ayşegül Gözen
Biology Department, METU _____

Assist. Prof. Dr. Ayşegül Birand
Biology Department, METU _____

Date: **10.02.2012**

I hereby declare that all information in this document has been obtained and presented in accordance with academic rules and ethical conduct. I also declare that, as required by these rules and conduct, I have fully cited and referenced all material and results that are not original to this work.

Name, Last Name : Ece Saraoğlu

Signature :

ABSTRACT

IMPACT OF WATER LEVEL FLUCTUATIONS AND FISH ON MACROINVERTEBRATE COMMUNITY AND PERIPHYTON GROWTH IN SHALLOW LAKES - A MESOCOSM APPROACH

Saraoğlu, Ece

M.S., Department of Biology

Supervisor: Prof. Dr. Meryem Beklioğlu Yerli

Co-Supervisor: Prof. Dr. Erik Jeppesen

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A mesocosm experiment was conducted in Lake Eymir between June – September 2009 in order to elucidate the effects of water level changes and fish predation on periphyton growth and macroinvertebrates in semi-arid shallow lakes.

Twenty four cylindrical enclosures, each with 1.2 m diameter, open to lake bottom and atmosphere, were placed at three different depths, i.e. 0.8 m (low water level, LW), 1.6 m (high water level, HW) and 2.3 m (however, data regarding the enclosures at 2.3 m were excluded in this study due to complications after fifth sampling) to simulate water level fluctuations. At each water level, four replicates were stocked with omnivorous–planktivorous fish (*Tinca tinca* and *Alburnus escherichii*) and the other four

replicates were left fishless to observe the effect of fish predation. Ten shoots of submerged macrophytes (*Potamogeton pectinatus*) were planted and six polyethylene strips were hung in the water column in each enclosure to monitor macrophyte and periphyton growth.

The mesocosms were sampled for physical, chemical and biological parameters weekly in the first month and fortnightly thereafter. Benthic macroinvertebrate samples were taken before the start, in the middle and at the end of the experiment with Kajak corer. Macrophytes were harvested after the last sampling for determination of dry weight, epiphyton, and the associated macroinvertebrates. All macroinvertebrate samples were sieved through 212 μm mesh size before identification and counting.

Over the course of the experiment, an average of 0.46 ± 0.03 m water level decrease in the mesocosms triggered submerged macrophyte growth in all LW enclosures, overriding the negative effects of fish predation. The results indicate that while fish predation pressure had negative influences on macroinvertebrate communities in terms of both abundance and richness, structural complexity created by dense vegetation in the LW mesocosms weakened the top-down effect of fish on macroinvertebrates by acting as a refuge in this semi-arid shallow lake.

Keywords: Macroinvertebrate, Periphyton, Water Level, Fish Predation, Mesocosm

ÖZ

SIĞ GÖLLERDE SU SEVİYESİ DEĞİŞİMİ VE BALIK BESLENMESİNİN MAKROOMURGASIZ TOPLULUKLARI VE PERİFİTON BÜYÜMESİ ÜZERİNDEKİ ETKİLERİ - *MEZOKOZM* YAKLAŞIMI

Saraoğlu, Ece

Yüksek Lisans, Biyoloji Bölümü

Tez Yöneticisi: Prof. Dr. Meryem Beklioğlu Yerli

Ortak Tez Yöneticisi: Prof. Dr. Erik Jeppesen

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Su seviyesi değişimi ve balık beslenmesinin yarı-kurak sığ göllerde perifiton büyümesi ve makroomurgasızlar üzerindeki etkilerini belirlemek amacıyla, Haziran – Eylül 2009 tarihleri arasında Eymir Gölü'nde bir *mezokozm* deneyi gerçekleştirilmiştir.

Her biri 1,2 m çapında, göl tabanına ve atmosfere açık olan silindir şeklindeki yirmi dört adet deney düzeneği 0,8 m (düşük su seviyesi, LW), 1,6 m (yüksek su seviyesi, HW) ve 2,3 m olmak üzere su seviyesi değişimini temsil eden üç farklı derinliğe yerleştirilmiştir (ancak beşinci örneklemeden sonra karşılaşılan sorun nedeniyle 2,3 m'deki düzeneklere ait veriler bu çalışmada kullanılmamıştır). Balık beslenmesinin etkisini gözlemlemek amacıyla, her bir su seviyesinde düzeneklerin dördüne omnivor-planktivor balıklar (*Tinca*

tinca ve *Alburnus escherichii*) eklenmiş, kalan dört düzenek ise balıksız olarak bırakılmıştır. Suiçi bitkisi ve perifiton büyümesini izlemek amacıyla tüm düzeneklerin içine onar adet suiçi bitkisi (*Potamogeton pectinatus*) filizi ekilmiş ve altışar adet polietilen şerit yerleştirilmiştir.

Fiziksel, kimyasal ve biyolojik parametreler ilk ay haftalık olarak, deneyin geri kalanında ise iki haftada bir örneklenmiştir. Bentik makroomurgasız örnekleri deneyin başında, ortasında ve sonunda Kajak tipi karotiyer ile alınmıştır. Bitki kuru ağırlığı ve epifit miktarının belirlenmesi amacıyla suiçi bitkileri son örneklemeden sonra toplanmış ve üzerindeki makroomurgasızlar örneklenmiştir. Taksonomik sınıflandırma ve sayım için tüm makroomurgasız örnekleri 212 µm'lik elekten geçirilmiştir.

Deney süresince *mezokozm*lardaki ortalama 0,46 ± 0,03 m'lik su seviyesi düşüşü balık beslenmesinin olumsuz etkilerini telafi ederek, düşük su seviyesindeki (LW) tüm düzeneklerde suiçi bitkilerinin büyümesini sağlamıştır. Elde edilen sonuçlar, yarı-kurak sığ göllerde balık avlanma baskısının makroomurgasız toplulukları üzerinde hem yoğunluk hem de çeşitlilik açısından olumsuz etkileri olurken; LW düzeneklerinde su seviyesi düşüşüyle desteklenen yoğun bitki gelişiminin sığınak rolü üstlenerek, balıkların makroomurgasızlar üzerindeki yukarıdan aşağıya kontrolünü zayıflattığını göstermektedir.

Anahtar Kelimeler: Makroomurgasız, Perifiton, Su Seviyesi, Balık Beslenmesi, *Mezokozm*

To my dear friends Seza Bürkan & Utku

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LIST OF ABBREVIATIONS

ANOVA	Analysis of variance
DW	Dry weight
chl-*a*	chlorophyll-*a*
F	Fish
HW-	High water level fishless
HW+	High water level with fish
LW-	Low water level fishless
LW+	Low water level with fish
SD	Standard deviation
SE	Standard e
WL	Water level
WLF	Water level fluctuations

CHAPTER 1

INTRODUCTION

1.1 Shallow Lakes at a Glance

Freshwater lakes, though they comprise only a minor fraction (approximately 0.009 %) of the total available water in the Biosphere, are vital for terrestrial life and fundamentally important hosts to rich biodiversity, thanks to their littoral zone (Wetzel, 2001). Moreover, lentic ecosystems provide many goods, materials and services to human beings, such as freshwater resources for drinking, consumption and irrigation, fish stocks, recreation, and so forth. However, misuse and overexploitation have led to deterioration of these vulnerable ecosystems, especially after the industrial revolution.

Basins of large, deep lakes contain a considerable volume (almost 40%) of the total available fresh water, and historically they have received much scientific attention (Wetzel, 2001; Meerhoff, 2010). However, most of the millions of lakes on earth (approximately 95%) are small (surface area <1 km^2) and relatively shallow (mean depth <10 m) (Wetzel, 2001). Over the last couple of decades, the scientific interest in shallow lakes has accelerated worldwide (Meerhoff, 2010).

Wetzel (2001) defined a shallow lake as a permanent standing body of water that is sufficiently shallow to allow light penetration to the bottom sediments adequate to potentially support photosynthesis of higher aquatic plants over

the entire basin. Shallow lakes usually do not experience thermal stratification. They are characterized by a larger area for the interaction of sediment-water interface and a higher rate of internal nutrients recycling. Accordingly, they possess a larger littoral area, more abundant macrophytes and usually a higher productivity per unit area of water than deep lakes (Gasith & Hoyer, 1998; Moss, 1998; Wetzel, 2001). For this reason, shallow lakes are crucial for the conservation of local and global biodiversity, though their conservation value as a biodiversity resource is often overlooked.

Over a wide range of nutrient concentrations, shallow lakes can exist in two alternative equilibria, i.e. macrophyte dominated clear water state and phytoplankton dominated turbid water state. Shifts between these states may have substantial impacts on ecosystems (Scheffer et al., 1993). Both states are stable and triggered by several feedback mechanisms related to biological interactions and physico-chemical processes. These mechanisms are needed to be surpassed for a shift between the two states to occur (Blindow et al., 1993; Scheffer et al., 1993; Scheffer, 1998).

When the nutrient concentrations are low, the lake is in a clear water state characterized by dense macrophyte beds and low chlorophyll concentrations. As compared to lakes without vegetation, vegetated lakes host richer biodiversity, with abundance of invertebrates, fish and waterfowl (Scheffer et al., 2006). Macrophytes provide refuge against predation by creating heterogeneity, alter the nutrient dynamics of the system, prevent resuspension of the sediment and enhance water clarity (Scheffer et al., 1993). However, the lake may shift to an alternative equilibrium of phytoplankton dominance and high chlorophyll concentrations. Nutrient runoff caused by intensive agricultural practices and sewage disposal from anthropogenic sources has lead to intensification of the eutrophication phenomenon (Jeppesen, 1998), which is defined as the shift in the trophic status of a water body towards a great increase in phytoplankton in response

to increased nitrogen (N) and phosphorous (P) loading. This eventuates in deterioration of water clarity and loss of ecological and conservation values of water bodies through elimination of predatory fish, submerged plants and waterfowl (Scheffer et al., 1993).

Various abiotic factors and biotic processes act at different spatial and temporal scales to shape the functioning and dynamics of shallow lakes. Some of the most important abiotic factors are lake morphology, hydrology, catchment and sediment characteristics, nutrient and light availability, oxygen concentration, pH and temperature. Once these factors set the background for the lake environment, biotic interactions such as predation and competition for resources take the stage to determine the community composition. Organisms affect each other either directly or through more complex interactions (Brönmark & Hansson, 2002). This study focuses on two of these variables, i.e. fish predation and changes in water level, and their effects on macroinvertebrates will be discussed further in the following sections.

Most studies about the functioning of shallow lakes have concentrated on the northern temperate regions. However, recent studies have revealed that the functioning of warmer shallow lakes differs from that of northern temperate lakes. Shallow lakes in the subtropical regions and the semi-arid Mediterranean basin exhibit contrasting characteristics such as prevalent omnivory, weakened role of macrophytes as refuge, and higher abundance of fish with smaller body size, especially through the plant beds (Meerhoff, 2006). The anticipated effects of global climate change on these lake ecosystems accentuate the importance of scientific research on them (Coops et al., 2003).

1.2 Climate Change Effects on the Mediterranean Shallow Lakes

The term "climate change" indicates a change of climate in addition to natural climate variability observed over comparable time periods, and it is attributed directly or indirectly to human activity that alters the composition of the global atmosphere (UNFCCC, 2011).

As a result of burning greater amounts of fossil fuels after the industrial revolution, deforestation and urbanization, the increasing greenhouse gas concentrations in the atmosphere have intensified the greenhouse effect, which has caused the average temperature of the Earth's surface to rise by 0.74°C since the late 1800s (UNFCCC, 2011).

Observational evidence from all continents and most oceans has shown that many physical and biological systems are being altered by recent regional changes in climate, particularly temperature increases. Freshwater ecosystems are particularly vulnerable as the altered precipitation patterns and evaporation rates will have a substantial destabilizing effect on the hydrologic cycle (IPCC, 2007). Climate is of great importance for lake hydrology as it determines the water inputs, outputs and residence time (Coops et al., 2003). In many regions, warming is occurring in lakes and rivers with discernible effects on thermal structure and water quality. Changes are observed in freshwater biological systems associated with rising water temperatures. The main impacts projected for climate changes concerning water resources in mid-latitudes and semi-arid low latitudes are decreasing water availability and increasing drought (IPCC, 2007).

Owing to their large surface area to volume ratio, changes in air temperature are reflected closely in water temperatures of shallow lakes. For this reason, shallow lakes are particularly sensitive to climatic changes, and they are expected to be highly influenced by the global climate change. Scientific evidence suggests that the effects of eutrophication may be intensified by

climate warming, which may result in the elimination of submerged plants, predatory fish and waterfowl, leading to deterioration of water clarity and loss of ecological and conservation values of shallow lakes (Scheffer et al., 1993; Jeppesen et al., 2007).

As mentioned in the previous section, scientific research has historically concentrated on the temperate lakes of the northern hemisphere climatic regions. However, climate model projections for the twenty-first century and current scientific data reveal that these lakes are in a warming trend (Meerhoff, 2006). Thus the lakes in the warmer regions of the world have lately caught attention as they can offer an insight as to how the temperate lake dynamics can be like under a warming climate. Moreover, some of the regions in mid-latitudes and semi-arid low latitudes are already water stressed areas. Therefore, the lake dynamics in these regions should be well understood in order to make sound management plans and to be prepared for the devastating effects of global climate change on shallow lake ecosystems.

The Mediterranean climate is characterized by mild and wet winters and hot and dry summer seasons (Giannakopoulos, 2005). The Mediterranean is projected to be a potentially vulnerable region to climatic changes (Sánchez et al., 2004). Results of global and regional climate model simulations (A1B scenario of IPCC for the period 2071–2100, compared to the period 1961–1990) project that the region is likely to experience a general reduction in precipitation (up to 30%), and an increase in surface air temperature (up to 5°C) especially in the warm season. Inter-annual variability as well as the occurrence of extreme heat and drought events is also projected to increase (Giannakopoulos, 2005; Giorgi, 2008). Accordingly, the lakes in this region are predicted to receive less water input due to shorter precipitation seasons coupled with higher incidence of droughts in summer (Coops et al., 2003; Beklioglu & Tan, 2008).

Being a country in the Mediterranean basin, Turkey is also expected to face the above mentioned climatic changes and damaging effects of global climate change on its vulnerable lake ecosystems as most of the 900 natural lakes and ponds in Turkey are shallow and have large surface areas (Coops et al., 2003).

1.3 Macroinvertebrates in Shallow Lake Ecosystems

Macroinvertebrates are distinguished from other invertebrates with their body size exceeding 0.5 mm, and are large enough to be seen by the naked eye (Jacobsen, 2008). Being very diverse both taxonomically and functionally, and highly variable geographically and seasonally, macroinvertebrates are among the organisms showing highest diversity in freshwater habitats (Boll, 2010).

As a crucial component of the food web of lakes, lentic macroinvertebrates play an important role in the sequestration and recycling of materials (Schindler & Scheuerell, 2002; Donohue et al., 2009), and in linking the benthic and pelagic compartments of lacustrine ecosystems (Vander Zanden & Vadeboncoeur, 2002; Jones & Waldron, 2003). Notwithstanding all these features, their interactions with the organic and inorganic components of shallow lake ecosystems has received relatively less scientific interest as compared to other groups of organisms such as fish, macrophytes and zooplankton.

Littoral macroinvertebrate communities can be classified according to the microhabitats they use, as benthic (i.e. those dwelling bottom sediments), epiphytic (i.e. those associated with macrophyte surfaces) and open water (Diehl & Kornijów, 1998; Kornijów et al., 2005). Shallow lakes form a crucial habitat for many benthic and epiphytic macroinvertebrate communities, such as insect larvae and nymphs. They constitute a substantial biomass and have a significant role in overall production (Free et al., 2009).

Given that macroinvertebrate communities respond to a diverse series of environmental conditions with their high variability and complexity, act as a vital link in aquatic food chains, have life cycles long enough to determine short-term temporal disturbances, are composed of diverse functional feeding groups, sensitive to water quality, confined to specific area and easy to sample, they have long been used in biomonitoring studies (White et al., 2008; Donohue et al., 2009; Free et al., 2009). Their importance as biological indicators for assessing the ecological status of lakes has been increasingly gaining attention (Moss et al., 2003; García-Criado et al., 2005; Free et al., 2009) since the enactment of the Water Framework Directive (2000/60/EC) by the European Union (Council of the European Communities, 2000).

Both bottom-up and top-down forces shape the macroinvertebrate communities in shallow lakes directly and indirectly. Several studies have been conducted in order to determine the effects of abiotic and biotic factors on macroinvertebrate communities at both within-lake and among-lake scales (Eriksson et al., 1980; Gilinsky, 1984; Diehl, 1992; Jackson & Harvey, 1993; Baumgärtner et al., 2008; Beresford & Jones, 2010). Biotic factors such as predator-prey interactions, competition and life-history traits play a major role in structuring community composition at within-lake scale (Gilinsky, 1984; Johnson et al., 1996). The influences of water level fluctuations and fish predation on macroinvertebrates will be discussed in more detail in sections 1.3.1 and 1.3.2, respectively.

1.3.1 Water Level Fluctuations

Hydrology is a critical abiotic factor in determining the functioning of shallow lakes, especially of those located in the arid and semi-arid regions which are highly susceptible to the changes in water level and input. Water level fluctuations with high amplitude (i.e. the difference between maximum and

minimum water levels) are common in the Mediterranean region where inadequate water input by precipitation mainly in winter season fails to balance high evaporative loss in summer (Beklioglu et al., 2006). Therefore, understanding the role of water level fluctuations in the functioning of shallow lake ecosystems has become particularly important given the recent concerns about global climate change, especially in the Mediterranean climatic region due to the predictions of a drier and hotter climate (Beklioglu & Tan, 2008).

Water level fluctuations may occur at different temporal scales ranging from short-term (e.g. wind-induced oscillations) to long-term (seasonal, annual, interannual and interdecadal). The amplitude of intra- and inter-annual water level fluctuations depends largely on the regional climate (e.g. temperate, semi-arid and arid) and catchment characteristics. Anthropogenic factors such as human water use and global climate change are expected to accentuate these fluctuations (Coops et al., 2003; Beklioglu et al., 2006).

Water level fluctuations may have overriding effects on the extent of light penetration (Leira & Cantonati, 2008) and water chemistry (i.e. salinity, nutrients, pH), and in turn, the ecology of shallow lakes, particularly on submerged plant development (Coops et al., 2003; Beklioglu et al., 2006). Fluctuation of water levels and extremes may cause shifts between the two alternative stable states (Coops et al., 2003; Beklioglu et al., 2006; Beklioglu et al., 2007). High water levels may result in the loss of submerged macrophytes by inhibiting sunlight radiation to reach to lower levels in the water column and cause a shift to phytoplankton dominated turbid state (Leira & Cantonati, 2008). Low water levels may cause a similar shift by damaging the vegetation via inducing desiccation during summer, and mediating freezing of the lake bottom and wave action during winter (Blindow et al., 1993; Coops et al., 2003; Beklioglu et al., 2006). In contrast, benthic fish kills due to anoxic conditions at low water levels during summer or winter may initiate a shift to

macrophyte dominated clear water state (Leira & Cantonati, 2008). Such state shifts may in turn alter macroinvertebrate species richness and abundance via complex interactions between the trophic levels.

As mentioned in section 1.2, in the Mediterranean shallow lakes, macrophyte development may be enhanced by drops in spring water levels coupled with higher evaporation in summer and lower precipitation brought about by climate warming (Coops et al., 2003; Beklioglu et al., 2006). Though, it is argued that rising nutrient levels may counteract this situation (Beklioglu & Tan, 2008).

Fluctuating water levels may directly and indirectly affect the biomass and distribution of macroinvertebrate communities. Most of the studies are concentrated on the impact of water level regulation on macroinvertebrates in reservoirs or comparison of regulated and unregulated lakes in terms of their macroinvertebrate faunas (Hunt & Jones, 1972; Valdovinos et al., 2007; Aroviita & Hämäläinen, 2008). A direct negative impact of water level fluctuations on benthic macroinvertebrates is that they may become stranded and desiccate with drawdown in the littoral zone (McEwen & Butler, 2010). Water level fluctuations may also affect macroinvertebrates indirectly by altering macrophyte and epilithic/periphytic algal communities, which serve as refuge and food source for them. Strong relationships are reported between macroinvertebrates and macrophytes (Free et al., 2009). In shallow lakes, macroinvertebrates may benefit from water level fluctuations in mainly two ways:

First, as mentioned above, macrophyte growth stimulated by lower water levels can generate spatial heterogeneity and structural complexity. Submerged macrophytes provide shelter, habitat and refuge for macroinvertebrates against fish predation, thereby decreasing the strength of top-down effect of fish on macroinvertebrate communities (Kornijów et al., 2005; Free et al., 2009). Although several studies indicate that fish with

smaller size aggregate in high numbers within macrophytes in warm lakes (Meerhoff, 2006), dense vegetation may still act as a potential refuge for macroinvertebrates.

Secondly, various macroinvertebrate communities may utilize macrophytes and periphyton as important food sources. Periphyton is a complex community composed of algae, protozoa, fungi, bacteria, animal inorganic matter and organic detritus that is attached to the substrates in the water column, and periphyton growing on submerged macrophytes is called epiphyton (Wetzel, 2001; Jones & Sayer, 2003). Epiphyton and fresh macrophyte tissues make up an important part of the diets of some grazers. Shredders and deposit feeders feed on detritus formed by decaying epiphytic algae and macrophytes (Kornijów et al., 1995; Diehl & Kornijów, 1998).

1.3.2 Fish Predation

Macroinvertebrates provide an important food source for fish and enable ontogenetic shifts in their diet, and they thus have a considerable impact on the structure of fish communities (Diehl & Kornijów, 1998). In turn, fish significantly influence the structure of macroinvertebrate communities of lakes (Jones & Sayer, 2003). Fish predation can cause differences in the size (Post & Cucin, 1984; Mittelbach, 1988), biomass (Post & Cucin, 1984; Diehl, 1992; Diehl & Kornijów, 1998; Jones et al., 2002; Williams et al., 2002), community composition (Langdon et al., 2010) and behaviour (Marklund et al., 2001) of macroinvertebrates.

Presence or absence of fish plays a determinant role in the existence of several macroinvertebrate taxa in lakes, especially Chaoboridae, Corixidae, Dytiscidae and Notonectidae (Bendell & McNicol, 1987). Larger and more motile taxa are known to be immediately consumed by fish (Crowder & Cooper, 1982; Mittelbach, 1988; Diehl, 1992; Leppä et al., 2003; Beresford &

Jones, 2010; Boll, 2010). Thus, some aquatic insect assemblages unique to naturally fishless lakes have been identified as bioindicators of fish absence (Schilling et al., 2009). Besides, macroinvertebrates are also used in determination of naturally fishless lakes by palaeolimnological techniques (Schilling et al., 2008).

Effects of fish predation on the abundance, richness and size distribution of macroinvertebrates have been studied in a number of enclosure and exclosure experiments (Brönmark, 1994; Batzer et al., 2000) but only a few of these studies principally consider the nonmolluscan macroinvertebrates (i.e. those other than herbivorous mollusks such as snails).

Fish predation pressure on macroinvertebrates can induce trophic cascades. Fish may indirectly promote epiphyton growth by preying upon macrophyte-associated grazing macroinvertebrates, such as snails (Jones & Sayer, 2003). In a nutrient-rich lake, this may trigger a shift to turbid state via out-shading of submerged macrophytes by periphyton (Scheffer et al., 1993).

As a climate change scenario, diminishing of piscivorous fish and in turn reduced top-down control on plankti-benthivores and higher degree of omnivory, longer spawning season with declining latitude, fish with smaller size, frequent reproduction, higher specific metabolic and excretion rates may imply higher predation pressure on macroinvertebrates with rising temperatures (Meerhoff, 2006).

1.4 Scope of the Study

Mesocosm approach is a valuable tool for understanding the responses of community structures to various factors by allowing control and manipulation of parameters together with replication. The mesocosm experiment was carried out with the main scope of determining the individual

and combined effects of water level fluctuations and fish predation pressure on the ecosystem dynamics and growth of submerged macrophytes in semi-arid shallow eutrophic lakes. Bucak (2011) showed that water level was critical for submerged plant growth; the decrease in water levels and a corresponding increase in underwater light availability compensated for the unfavourable effects of fish on macrophyte development.

Accordingly, this thesis study aims to elucidate the relative influences of water level changes and fish on periphyton growth and macroinvertebrates by manipulating fish presence at different water levels in the *in situ* mesocosms. We hypothesized that macroinvertebrate community structure would be adversely affected by top-down control whereas a decline in water level and a corresponding macrophyte growth and periphyton development would, even at presence of fish predation, favor macroinvertebrates by providing refuge and food source.

In order to test this hypothesis, the experiment was carried out in a shallow Mediterranean lake, Lake Eymir, using mesocosms constructed at three different depths reflecting a possible water level fluctuation in the presence and absence of fish.

CHAPTER 2

MATERIALS & METHODS

2.1 Study Site

The mesocosm experiment was conducted in Lake Eymir. Lake Eymir is a eutrophic shallow lake located south of Ankara, in the Central Anatolia Region of Turkey (39° 57′ N, 32° 53′ E) (Beklioglu et al., 2003). The morphometric and hydrological characteristics of the lake are summarized in Table 1.

The region experiences the Central Anatolian semi-arid climatic conditions, the characteristics of which are hot and dry summers, the precipitation mostly falling in winter and spring. Accordingly, minimum water levels occur during summer because of evaporation, and maximum depths are reached during autumn-winter as a result of intense rainfall and snow fall. Frosts are common during winter months. Average annual air temperature and precipitation are 21.5 ± 0.8°C and 384 ± 104 mm, respectively, for a period of thirty years (1975-2006) (Özen et al., 2010). The lake experienced rainfall at the beginning of the summer season, but occasional showers towards the end of the sampling period, with evaporation becoming more significant in parallel with the rising temperatures.

A nearby larger shallow lake, Lake Mogan is interconnected to the downstream Lake Eymir. The outflow from Lake Mogan constitutes the main inflow of Lake Eymir ("E inflow I" in Figure 1) (Beklioglu et al., 2003), though

the canal connecting the two lakes had not been flowing for the last few years including the sampling period. Another inflow to the lake is Kışlakçı Brook ("E inflow II" in Figure 1), which feeds the lake in late winter and spring, and dries in summer. The water leaves via an outflow at the northern tip of Lake Eymir ("E outflow" in Figure 1).

Table 1: Morphometric and hydrological characteristics of Lake Eymir (Beklioglu et al., 2003; Özen et al., 2010)

Catchment area	971 km^2
Altitude	900 m a.s.l.
Surface area	1.20 – 1.25 km^2
Volume	3.88×10^6 m^3
Mean depth	2.6 – 3.2 m
Maximum depth	4.3 – 6 m
Shoreline	13 km
Hydraulic retention time	0.2 – 13.5 yr
Water level fluctuation (mean amplitude of the period 1993–2007)	0.9 ± 0.3 m a.s.l.

More than half a century ago, Lake Eymir was in a clear water state, dominated by dense submerged plant beds (mainly Charophytes, colonization depth of which reached a maximum of 6-7 m out of 8 m of maximum water depth) and nine Cladocera species, including three species of large-bodied daphnids (Geldiay, 1949). At the time, a Secchi disc transparency of more than 4 m was measured in summer (Geldiay, 1949). Nonetheless, untreated sewage effluent discharge to the main inflow resulted in a decrease in lake water quality after 1970s. Total phosphorous (TP), dissolved inorganic nitrogen (DIN), chlorophyll-*a* and suspended solids (SS) concentrations remained at very high levels and Secchi disc depth was low until the sewage effluent diversion in 1995. The diversion caused a significant decrease in TP and DIN concentrations, but the water quality and submerged plant coverage

remained low (Beklioglu et al., 2003). Following the sewerage diversion, the lake was subjected to biomanipulation between 1998 and 1999. About half of the planktivorous tench (*Tinca tinca*, Linnaeus 1758) and the benthivorous common carp (*Cyprinus carpio*, Linnaeus 1758) stock was taken out of Lake Eymir, which had a considerable effect on water quality (Beklioglu et al., 2003). Lowered chlorophyll-*a* and inorganic SS concentrations and enhanced Secchi disc depth resulted in the expansion of surface submerged macrophyte coverage up to 40-90% beginning from 2000 until 2003 (Beklioglu & Tan, 2008). Upon the shift of the lake back to turbid water state in 2004 due to the increase in benthi-planktivorous fish stock, and the disappearance of submerged plants, a second biomanipulation attempt was undertaken in 2006-2007. Removal of tench and common carp restored the lake water quality, however poor macrophyte coverage persisted (Özen et al., 2010).

Currently, the fish stock is dominated by *Tinca tinca*, *Cyprinus carpio* and stone moroko, *Pseudorasbora parva* (Temminck & Schlegel, 1846). The macrophyte community is mainly composed of sago pondweed, *Potamogeton pectinatus* (Linnaeus, 1753) and *Najas* sp. The phytoplankton community is dominated by chlorophytes during the clear water period and by cyanobacteria during the turbid period. *Daphnia pulex* (De Geer, 1776) and *Arctodiaptomus bacillifer* (Koelbel, 1885) largely dominates the zooplankton community. The dominant emergent plant is common reed, *Phragmites australis* (Cavanilles) Trinius ex Steudel on the shoreline (Beklioglu et al., unpublished data).

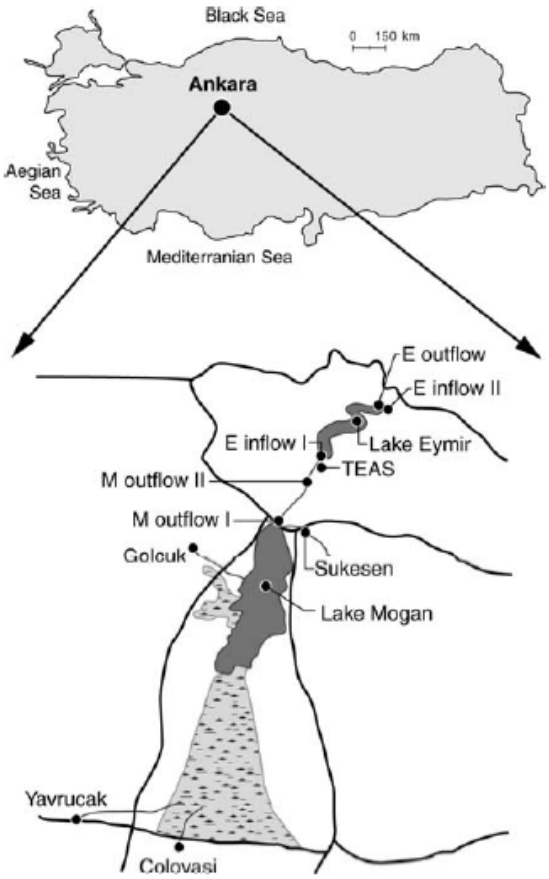

Figure 1: Inflows and outflows of the study site, Lake Eymir, and its upstream lake, Lake Mogan, and the location of the lakes on the map of Turkey (taken from Özen *et al.*, 2010)

2.2 Experimental Setup: Mesocosms

The experimental setup consisted of cylindrical enclosures that were isolated from the lake, but exposed to the lake sediment and the atmosphere. Each enclosure had 1.2 m diameter. The wall of each enclosure was made of transparent, nylon-reinforced impermeable polyethylene (PE) tube with 0.18 mm thickness so as to enable the penetration of sunlight through the water column inside. The PE tubes were attached to metal rings on the lower end and to polyvinyl chloride (PVC) rings on the upper end by using cable ties and duct tape. The bottom rings were manually extended approximately 0.3 m

into the muddy sediment by scuba divers. The top rings were kept floating 0.3 m above the water surface by aluminum floating frames. Each segment of the frame had a dimension of 1.2 m × 1.2 m × 0.3 m (Özkan, 2008) and the whole frame consisted of 4 segments on two rows, making up a structure with 5 m length and 2.5 m width. The lower part of the aluminum frame was supported with elongated polyurethane (PU) foams to enable buoyancy of the frame and the attached upper rings of the enclosures above the lake surface. The experimental setup was kept stable in the lake by fixing the frames from each corner to concrete bricks placed at the lake bottom using durable ropes. An enclosure is illustrated in Figure 2.

The enclosures and the aluminum frame were constructed on land and transported to the experiment location by means of an inflatable boat. All natural vegetation was carefully removed from the lake bottom by scuba divers using hand rakes at each mesocosm site prior to the placement of the experimental setup. Following the placement and anchoring of the aluminum frames, the enclosures were lowered one by one through each segment of the frame into the water and their top rings were fixed to the upper part of the frame using cable ties by scuba divers. Fish intrusion into the enclosures was prevented during the construction and checked by scuba divers. After the establishment of the enclosures, the setup was left for one week prior to the first sampling so that the turbidity arising from the mesocosm asemblage could settle down and the water column become stable. The enclosures were carefully checked for possible fish presence using underwater binoculars in the meantime.

Potamageton pectinatus, a common macrophyte species of the lake's flora, was harvested from the lake. Ten shoots of *P. pectinatus* were transplanted to each enclosure. Each of them had healthy roots, similar length and number of shoots in order to achieve similar initial plant densities in the enclosures. Pebbles were placed in small nylon bags and strings stamped to them were

gently tied to the roots of the shoots so that they could sink to the bottom and remain in contact with the sediment. Each enclosure was inoculated with the same amount (about 1 L of volume) of zooplankton collected from Lake Eymir with 50 μm mesh-size plankton net.

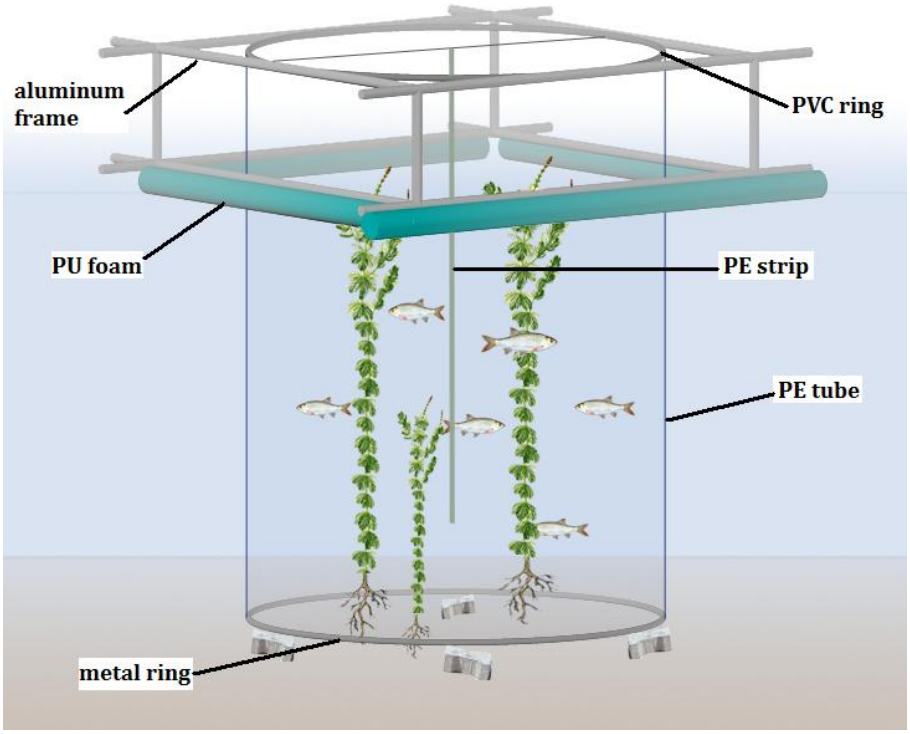

Figure 2: An illustration of the mesocosm setup (taken from Özkan, 2008)

In order to monitor periphyton growth, in each enclosure six PE strips made of the same material as the enclosure walls were hung from a string attached to the upper part of the aluminum frame across the enclosure diameter, through the water column with a weight attached to the lower tip of the strip. Each strip had a length equal to the water depth and 3 cm width.

All enclosures were covered with nylon netting having fine (1 cm × 1 cm) mesh size to deter any interference from outside the mesocosms, such as frog or water snake intrusion, bird predation on macrophytes or fish. The

establishment phases of the mesocosm and the close-up view of an enclosure are given in Figure 3 and Figure 4, respectively.

The mesocosm experiment was proposed as 2 × 3 full factorial replicated block design with four replicate enclosures per treatment, by leaving fishless versus adding fish to the enclosures established at three different water depths; 0.8 m, 1.6 m and 2.3 m, corresponding to low, medium and high water levels, respectively. The replicated treatments were distributed randomly in the floating frames at each water level. The frames at each depth included 8 enclosures, making up a total of 24 enclosures. The locations of the mesocosms are presented in Figure 5 showing the Google Earth image of Lake Eymir.

Fish were stocked to the enclosures after the first sampling. At each depth, twelve omnivorous–planktivorous fish from the lake's fauna, i.e. six tench, *Tinca tinca* and six bleak, *Alburnus escherichii* (Steindachner, 1987) having an average size of 6 cm were added to four replicates corresponding to the typical fish density of Lake Eymir (Beklioglu & Tan, 2008), and the other four replicates were left without fish. Fish were caught from the native populations in Lake Eymir by a sweep net and left in a keepnet for an adequate time before stocking in order to relieve the stress caused by fishing. The survival of fish in the enclosures was visually monitored in the course of the experiment using underwater binoculars. Dead fish were replaced with new ones when required.

Figure 3: Steps in mesocosm construction a) setting up cylindrical enclosures, b) assembling aluminum frames, c) attaching PU foams to frames, d) placing frames on site, e-f) installing and fixing mesocosms, g) planting macrophyte shoots, h) covering mesocosms with netting

As explained above, the experimental setup was established as a full factorial replicated block design, having two fish treatments and three water levels, with four replicates. However, three replicates in the fishless treatment at 2.3 m depth had to be cancelled due to complications encountered after the fifth sampling, and the only remaining replicate was not sampled during the rest of the experiment. Therefore, the results concerning the enclosures at 2.3 m are excluded in this study. Hereafter, the enclosures established at 0.8 m will be considered as "low water" (LW) and the ones at 1.6 m as "high water" (HW). The treatments with fish will be indicated by (+) sign while the fishless treatments will be indicated by (–) sign.

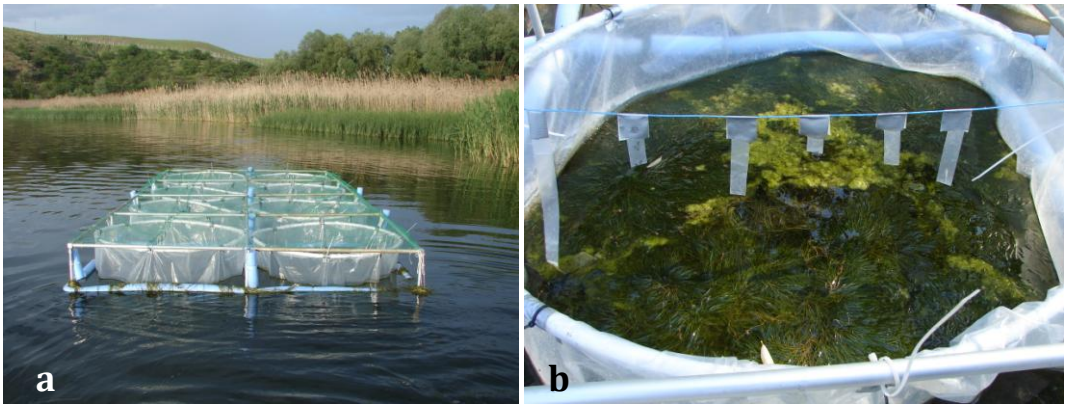

Figure 4: a) View from HW enclosures, b) Close-up view of a LW enclosure

Figure 5: Map of Lake Eymir and the locations of the mesocosms (Google Earth, 2011)

2.3 Sampling and Processing

The mesocosm experiment was conducted between May 26 – October 2, 2009 for four months so that the effects of different water levels and fish predation on submerged macrophyte growth could be observed in Lake Eymir. The sampling dates are given in Table 2. All samplings were performed from a small boat. The mesocosms were sampled for physical, chemical and biological parameters weekly in the first five samplings, and biweekly during the rest of the experiment. The first (pretreatment) sampling was performed prior to stocking of fish as a control tool to confirm the similarity of the initial conditions among the treatments and the replicates. On each sampling occasion, additional samples from outside the mesocosms at each water depth (from the open lake) were taken in addition to the samples in the mesocosms.

Table 2: Sampling dates

Sampling	1	2	3	4	5	6	7	8	9	10	11
Date	01.06.2009	09.06.2009	15.06.2009	22.06.2009	30.06.2009	13.07.2009	27.07.2009	06.08.2009	17.08.2009	10.09.2009	24.09.2009

Dissolved oxygen (DO) concentration, temperature, conductivity, total dissolved solids (TDS), salinity and pH were measured just below the water surface and at 0.5 m intervals (or 0.25 m intervals where necessary) through the water column with a YSI 556 MPS (Multi-Probe System) (Yellow Springs Incorporated, OH, U.S.A.) in each sampling.

Water depth, Secchi disc depth, percent macrophyte and filamentous algae coverage were also recorded for each enclosure. Water depth was measured

using both a Speedtech SM-5 Depthmate Portable Sounder Depth Meter and a sinker for maximum accuracy. Secchi depth was measured using a Secchi disc, paying attention to performing the measurements at the same time of the day for the same replicates. Plant volume infested (% PVI) for macrophyte development was calculated using water depth, average macrophyte height and surface coverage using the formula: PVI = % coverage × average height / water depth. Coverage estimation was performed by visually dividing the enclosure into quarters and estimating the area of the enclosure covered by plants (Canfield et al., 1984).

A 4 L composite sample was taken from the water column at each enclosure with a tube, avoiding disturbance to the periphyton strips, macrophytes or the sediment. A 0.5 L subsample of the composite water sample was taken for water chemistry analyses. A 0.4 L subsample was taken for suspended matter (SS) and chlorophyll *a* (chl-*a*) analyses. A 0.05 L subsample was preserved on site with 2 % Lugol's solution for phytoplankton identification. 3 L of the composite water sample was filtered through a 20-µm mesh size for zooplankton identification and preserved on site with 4 % Lugol's solution. In the field, all water chemistry, SS and chl-*a* samples were kept at dark and cold. They were put in the freezer as soon as arriving at the laboratory and kept frozen until the analyses have been carried out.

Starting from the third week, PE strips were sampled biweekly for periphyton chl-*a* analyses. In each sampling, one periphyton strip was taken out of the enclosure at a time with care not to disturb the attached periphyton. Two sections of the strip, each having 0.1 m length, located at 0.1–0.2 m below the water surface and 0.1–0.2 m above the lake bottom were cut with a scissor and kept in zip-lock bags in the dark. The remainder of the strips were also preserved in zip-lock bags in case of need for further analyses. They were frozen immediately upon arrival at the laboratory.

Benthic macroinvertebrate samples were taken before the start of the experiment, in the middle and at the end of the experiment. The dates of macroinvertebrate sampling are given in Table 3. Three replicates of the uppermost 10 cm of the sediment cores taken from each enclosure with a Kajak sediment core sampler having an internal diameter of 5.2 cm (Figure 6) were pooled together and put in plastic jars in the field. In the lab, they were sieved through 500 μm and 212 μm mesh sizes by rinsing the muddy fraction with tap water. However, no specimens were retained on the sieve with 500 μm mesh size. The benthic macroinvertebrates retained on the 212 μm mesh-size sieve were preserved in 70% ethanol for identification.

Macrophyte-associated macroinvertebrates were sampled only at the end of the experiment. The submerged macropytes grown at each enclosure were harvested at the end of the experiment using a hand rake. They were slowly taken out of water with care not to disturb the associated macroinvertebrates while a sieve was placed below them. The macropytes were taken into zip-lock bags. In the laboratory, they were thoroughly washed with tap water and the washing water was sieved through 500 μm and 212 μm mesh sizes to collect the associated macroinvertebrates. However, no specimens were retained on the sieve with 500 μm mesh size. The macrophyte-associated macroinvertebrate samples were preserved in 70% ethanol for identification. The macrophytes cleaned from the associated periphyton and macroinvertebrates were kept for dry weight determination.

The biomass of macrophyte-associated periphyton (hereafter called epiphyton) in each enclosure was determined at the end of the experiment. Three randomly chosen healthy shoots of each macrophte species of 10 cm length at least 5 cm under the water surface were carefully cut off, to avoid epiphyton disturbance and transferred into a PE bottle filled with tap water. Epiphyton was detached by shaking vigorously the bottle manually. Certain amount of the macrophyte-free water was filtered through Whatman GF/C

glass microfiber filter (Whatman International, Maidstone, U.K.) and the filters were submerged in ethanol for extraction (Jespersen & Christoffersen, 1987) in order to calculate the chl-*a* content of the epiphyton samples.

Sediment samples were taken with a Kajak corer at the end of the experiment for organic and carbonate content estimation of the sediment.

Table 3: Macroinvertebrate sampling dates

Sampling	Date	Sampled material
Initial sampling	26–27.05.2009	Benthic macroinvertebrates
Middle sampling	11–13.08.2009	Benthic macroinvertebrates
Final sampling	29–30.09.2009	Benthic macroinvertebrates
	02.10.2009	Macrophyte-associated macroinvertebrates

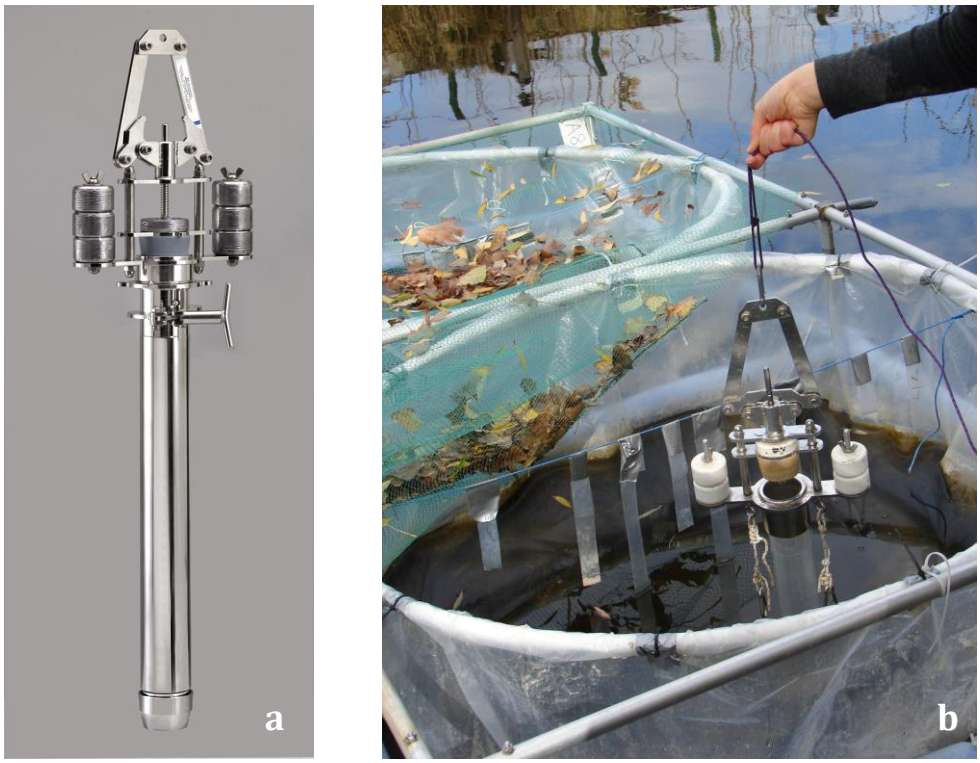

Figure 6: a) Kajak core sampler, b) View from benthic macroinvertebrate sampling

2.4 Laboratory Analysis

The water chemistry analyses were carried out immediately after thawing of the frozen samples. Total phosphorus (TP) and soluble reactive phosphorus (SRP) concentrations of the water samples were determined using standard methods based on molybdenum blue complex formation. Acid hydrolysis method was performed for TP analysis in unfiltered samples, and molybdate reaction method for SRP analysis in filtered samples (Mackereth et al., 1978). Analyses of the nitrogen-compounds, namely total nitrogen (TN), ammonium (NH_4-N) and nitrite-nitrate (NO_2-N and NO_3-N) were carried out with a continuous flow Skalar Autoanalyzer (San++ Automated Wet Chemistry Analyzer, Skalar Analytical, B.V., Breda, The Netherlands) following the standart methods (Krom, 1980; Searle, 1984; Houba et al., 1987; Kroon, 1993). All of the water chemistry analyses were conducted with two replicates of each sample.

Alkalinity analysis was performed with HCl titration of the samples using phenolphthalein and BDH indicators (Mackereth et al., 1978). Silicate content of the filtered samples was determined with molybdate reaction method (Golterman et al., 1978).

For estimation of chl-*a* pigment content of phytoplankton and amount of SS, known volumes of water samples were filtered onto Whatman GF/C glass microfiber filters. SS was determined as mg/L after drying the filter papers at 105°C for 12 hours and weighing (Clesceri et al., 1998). Chl-*a* was determined spectrophotometrically with ethanol extraction method at 663 and 750 nm wavelengths according to Jespersen & Christoffersen (1987) with triple replication. The same methodology was applied for the estimation of chl-*a* concentration associated with the periphyton strips.

The macropytes free of the associated periphyton and macroinvertebrates were dried at 105°C for 24 hours for determination of the macrophyte dry weight at the end of the experiment.

Sediment samples taken at the end of the experiment were treated according to the sequential loss on ignition (LOI) procedure (Dean, 1974; Heiri et al., 2001) for determining the water, organic matter and carbonate content of the sediment. Approximately 1 cc of the sediment samples taken from each enclosure were placed in preweighed ceramic crucibles and weighed. LOI of the samples was determined by measuring the weight loss after each heating step; i.e. 12 hours at 105°C to estimate the water content, then 2 hours at 550°C to estimate the organic matter content and finally, 4 hours at 925°C for carbonate content estimation. The crucibles were kept in a desiccator to cool completely before all weighing sessions.

The benthic macroinvertebrate samples were counted and identified under the stereo microscope (Leica MZ12.5, Leica MZ16 and Leica M125) at highest 100× magnification to the lowest taxonomic level possible following keys of Macan (1972), Quigley (1977), Fitter & Manuel (1995) and Nilsson (1996, 1997).

Since the macrophyte-associated macroinvertebrate samples contained great amounts of coarse particulate organic matter (CPOM) such as filamentous algae and plant pieces, samples were painstakingly cleaned of these nuisances on a sorting tray by visual checking with the aid of a magnifying glass. The samples were examined twice in order not to miss any small specimens. Because picking macroinvertebrates from CPOM-rich samples was a laborious job and this subsequently required a time-consuming sorting procedure, three out of four replicates from LW+ and LW– treatments were counted together with one HW+ and two HW– treatments in which plants had developed (i.e. a total of two samples were not counted). After this preliminary sorting process, the collected macroinvertebrates were counted

and identified under the stereo microscope (Leica MZ16 and Leica M125) at highest 100× magnification using the same keys for taxonomical identification.

Subsampling method was not employed in order to avoid substantial information loss and the whole samples were handled for counting (Vinson & Hawkins, 1996). Part of the benthic macroinvertebrate samples were counted and identified at National Environmental Research Institute of Denmark; macrophyte-associated macroinvertebrates and the rest of the benthic macroinvertebrates were counted and identified at METU Limnology Laboratory.

2.5 Statistical Analysis

The statistical analyses were performed with SigmaStat® release 3.5 (Systat Software, San Jose, CA/Richmond, CA, USA) and SAS® (Statistical Analysis Software) release 9.2 (SAS Institute Inc, Cary, NC) statistical softwares. The general linear model (GLM) procedure of SAS was used for repeated measures of two-way analysis of variance (RM two-way ANOVA) (Bucak, 2011) and SigmaStat was used for all the other analyses. Differences were considered statistically significant at the $p < 0.05$ level in all statistical analyses.

To assess similarity of the starting conditions in the mesocosms, initial sampling data regarding the physico-chemical parameters and chl-*a* were tested in one-way ANOVA, with water level as a fixed factor (Bucak, 2011). Since the initial sampling of benthic macroinvertebrates was also performed prior to fish addition, data regarding this sampling event was analysed with one-way ANOVA to test if there was any significant difference among the LW and HW treatments. The middle and final sampling data of benthic macroinvertebrates, epiphyton chl-*a*, macrophyte DW and macrophyte-

associated macroinvertebrate data were analysed with two-way ANOVA with water level and fish presence/absence as crossed fixed factors. In addition, the middle and final sampling data of benthic macroinvertebrates were handled using paired *t*-test (with Bonferroni correction of $\alpha = 0.0125$) in order to detect any significant effect of time between the two consecutive sampling events. Periphyton chl-*a* and PVI data were analysed with RM two-way ANOVA (Bucak, 2011). LOI data was tested in one-way ANOVA to see whether the sediment characteristics were significantly different in the LW and HW treatments. Tukey pairwise comparison test with 95% confidence level was applied in all statistical tests if the parameters showed significant difference.

Because of the nature of species-sample matrices with a high prevalence of zero entries, community data are likely to encounter major problems in fulfilling the assumptions for parametric statistics (Baumgärtner, Mörtl & Rothhaupt, 2008). Normal distribution of data was checked by the Kolmogorov–Smirnov goodness of fit procedure or relevant diagnostic plots. Data that violated normality or heteroscedasticity assumptions of ANOVA were logarithmic, square root or reciprocal transformed. The parameters that failed the assumptions even after $\log_{10}(x+1)$, $\sqrt{x}$ and $1/(x+1)$ transformations were analysed using the non-parametric analogues of the above mentioned parametric tests, namely Kruskal-Wallis and Friedman tests.

CHAPTER 3

RESULTS

3.1 Physico-chemical Parameters

During the course of the experiment, a significant water level drop was observed in all of the mesocosms, both LW and HW (Figure 7). At the start of the experiment, the water depth in LW enclosures ranged between 0.80-1 m, and in HW enclosures between 1.6-1.7 m. The difference in water depths between the initial and last sampling dates was 0.46 ± 0.03 m [mean ± standard deviation (SD)]. Water level decreased dramatically onward the fifth sampling, coinciding with the high surface water temperatures exceeding 26°C.

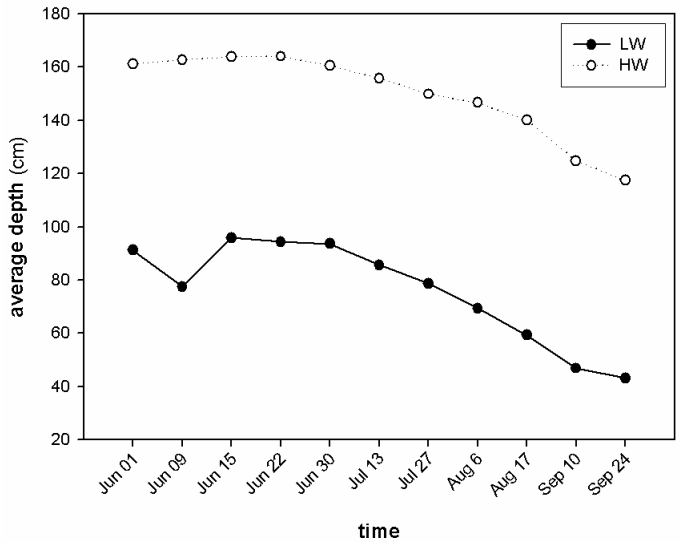

Figure 7: Change in water levels of the mesocosms over the course of the experiment

Initial conditions for all parameters are summarised in Table 4 according to the results of one-way ANOVA between LW and HW. Initial values of conductivity, TP and SRP differed significantly among the LW and HW treatments. RM two-way ANOVA results for all physico-chemical parameters and some of the biological variables are summarised in Table 5. The physico-chemical parameters are discussed thoroughly in Bucak (2011).

Table 4: One-way ANOVA results showing the influence of water level on the initial conditions of the parameters measured in time series and the parameters sampled once (denoted by asterisks) in the mesocosms (ns denotes a non-significant difference with $p > 0.05$.) (Bucak, 2011)

Parameter	***p***
Conductivity	<0.05
Suspended solids	ns
pH	ns
TP	0.003
SRP	<0.001
TN	ns
NO_2-N and NO_3-N	ns
chl-*a*	ns
Organic matter content (LOI at 550°C) *	ns
Carbonate content (LOI at 925°C) *	ns

As an indication of the extent of light penetration through the water column, the ratio of Secchi disc depth to average depth was used. Both water level and fish had a significant impact on this ratio (RM two-way ANOVA; p=0.004 and p=0.0001, respectively; Table 5) (Bucak, 2011). The Secchi disc depth/average depth ratio was higher in the fishless mesocosms through the experiment and converged to 1 (meaning Secchi disc depth was almost equal to the water level) in LW- mesocosms as a result of the enhanced underwater light penetration and decrease in water levels (Figure 8).

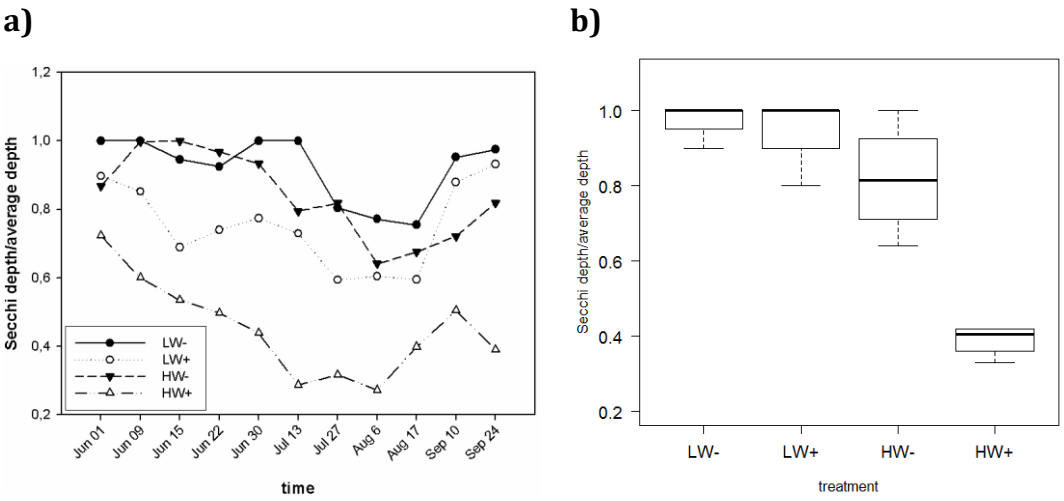

Figure 8: Ratio of Secchi disc depth to average depth of the mesocosms a) change over the course of the experiment, b) comparison of all treatments at the end of the experiment

3.2 Macrophytes, Epiphyton and Periphyton

Submerged macrophyte development remained very low in the HW mesocosms over the course of the experiment (Table 5; Figure 9). However, extensive macrophyte growth occurred in both the LW- and LW+ mesocosms, especially towards the end of the experiment (Table 5; Figure 9). Macrophytes grew not in all of the HW mesocosms and accordingly, the associated macroinvertebrates and epiphyton could only be sampled in three replicates of the HW mesocosms (i.e. two replicates in HW- and one replicate in HW+). PVI was significantly affected by both water level and fish (RM two-way ANOVA; $p<0.0001$ and $p=0.0001$, respectively; Table 5) (Bucak, 2011). Water level, fish and their interaction also significantly affected the dry weight of macrophytes harvested at the end of the experiment (two-way ANOVA; $p<0.0001$, $p=0.0243$, and $p=0.019$, respectively; Table 5 and Figure 9) (Bucak, 2011). LW- treatments had the highest macrophyte dry weight and %PVI at the end of the experiment.

Table 5: Average values [(mean ± standart error (SE)] of some physico-chemical and biological parameters measured in the mesocosms and the results of RM two-way ANOVA (only for macrophyte DW and epiphyton chl-*a*, which did not have time series data, *p* values are results of two-way ANOVA) (WL and F denote water level and fish, respectively. ns denotes a non-significant difference with *p* > 0.05.) (Bucak, 2011)

Parameter	mean ± SD				*p*		
	LW-	LW+	HW-	HW+	WL	F	WL*F
Secchi /average depth	0.92 ± 0.14	0.73 ± 0.21	0.84 ± 0.25	0.44 ± 0.21	0.004	0.0001	ns
Conductivity (µs/cm)	2862.2 ± 20.0	2802.1 ± 14.9	2721.4 ± 32.38	2716.8 ± 28.4	<0.0001	ns	0.001
Suspended solids (mg/L)	15.56 ± 1.24	34.02 ± 3.14	12.21 ± 1.36	25.18 ± 2.25	0.0114	<0.0001	ns
Dissolved oxygen (mg/L)	8.08 ± 0.40	6.74 ± 0.47	5.82 ± 0.54	5.38 ± 0.39	0.0005	ns	ns
pH	9.04 ± 0.03	8.81 ± 0.02	8.93 ± 0.02	8.88 ± 0.02	ns	0.0011	0.0202
TP (µg/L)	237.4 ± 11.37	269.8 ± 10.28	128.2 ± 10.34	179.2 ± 11.17	<0.0001	0.0128	ns
SRP (µg/L)	114.7 ± 7.59	114.2 ± 9.93	30.5 ± 2.64	41.0 ± 4.70	<0.001	ns	0.0424
TN (µg/L)	1312.3 ± 67.2	1506.8 ± 88.9	1176.3 ± 94.7	1214.6 ± 83.48	<0.001	0.0256	ns
NO2-N and NO3-N (µg/L)	31.88 ± 6.75	49.25 ± 9.16	10.13 ± 1.70	9.85 ± 1.87	0.0005	ns	ns
chl-a (µg/L)	15.58 ± 3.71	89.53 ± 14.26	19.35 ± 6.40	47.87 ± 7.31	0.025	<0.001	ns
Upper periphyton chl-a (µg/cm2)	4.87 ± 0.85	5.76 ± 0.75	4.24 ± 0.72	5.05 ± 0.89	ns	ns	ns
Lower periphyton chl-a (µg/cm2)	3.74 ± 0.51	4.17 ± 0.58	6.014 ± 0.62	2.09 ± 0.38	0.0003	0.0197	0.0046
PVI (%)	43.18 ± 5.16	24.33 ± 5.05	0.40 ± 0.22	1.47 ± 0.34	<0.0001	0.0001	ns
Macrophyte dry weight (g)	121.45 ± 22.64	58.73 ± 6.95	0.18 ± 0.11	1.74 ± 1.74	<0.0001	0.0243	0.019
Epiphyton chl-a (µg/g macrophyte DW)	0.83 ± 0.58	1.60 ± 0.84	7.61 ± 12.62	0.06 ± 0.12	0.01	ns	ns

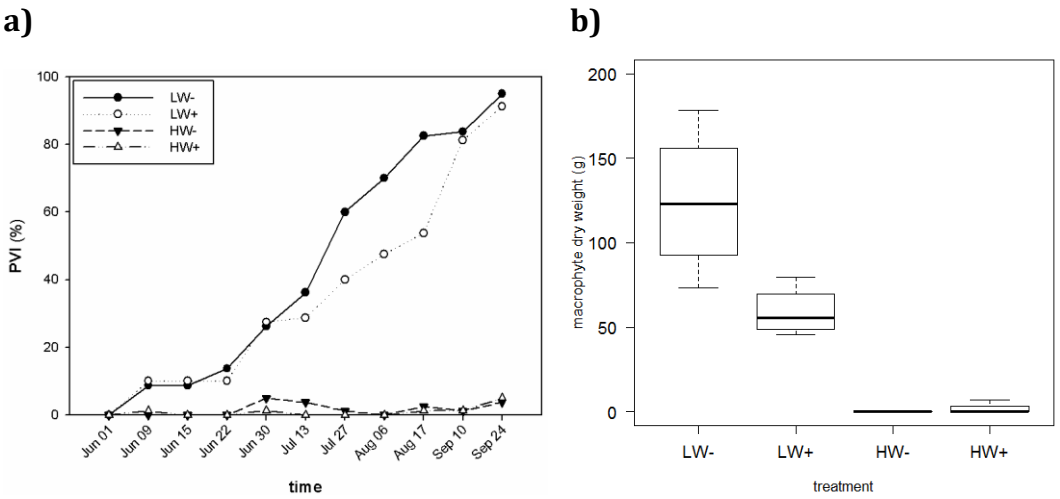

Figure 9: Macrophyte growth a) change in %PVI of the mesocosms over the course of the experiment, b) macrophyte DW in all treatments at the end of the experiment

Two-way ANOVA results indicate that the effect of water depth on epiphyton chl-*a* was significant (p=0.01; Table 5) as the epiphyton biomass in HW- enclosures was significantly higher than LW- enclosures (Tukey test, p=0.009). Overall, HW- treatments had the highest epiphyton biomass at the end of the experiment (Figure 10).

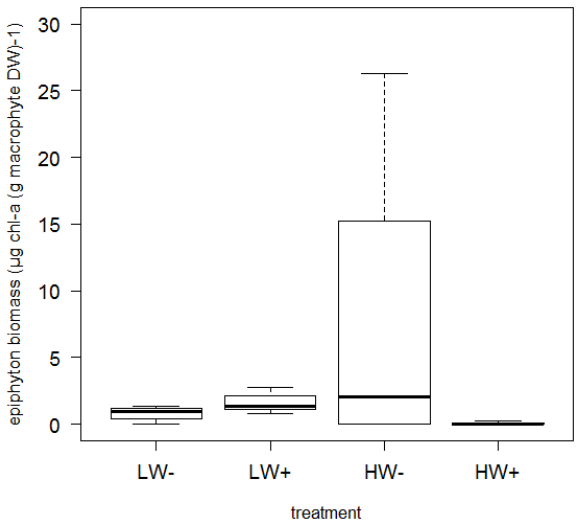

Figure 10: Epiphyton chl-*a* in all treatments at the end of the experiment

RM two-way ANOVA results (Table 5; Figure 11), showed no significant effect of neither water level nor fish (p>0.1 for both) on chl-*a* concentrations of the upper portion of periphyton strips (corresponding to 0.1–0.2 m below the water surface, hereafter called upper periphyton). On the contrary, both water level and fish were found to have a significant impact (p=0.0003 and p=0.0197, respectively) on chl-*a* concentrations of the lower portion of periphyton strips (corresponding to 0.1–0.2 m above the lake bottom, hereafter called bottom periphyton) according to the results of RM two-way ANOVA (Table 5; Figure 12). In addition, interaction of these two parameters also significantly affected the bottom periphyton biomass (p=0.0046) as it was highest in the HW- treatments at the end of the experiment (Figure 12).

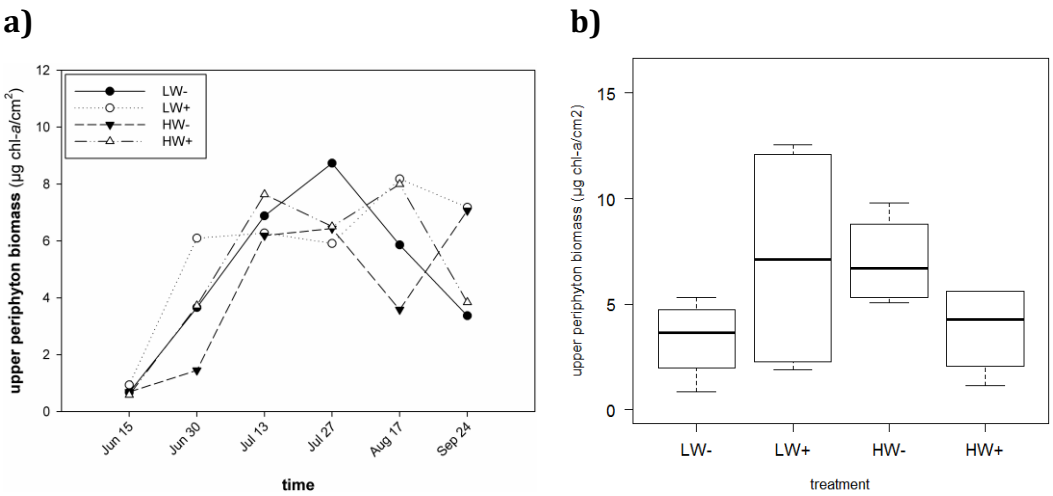

Figure 11: Upper periphyton chl-*a* a) change over the course of the experiment, b) comparison of all treatments in the last sampling

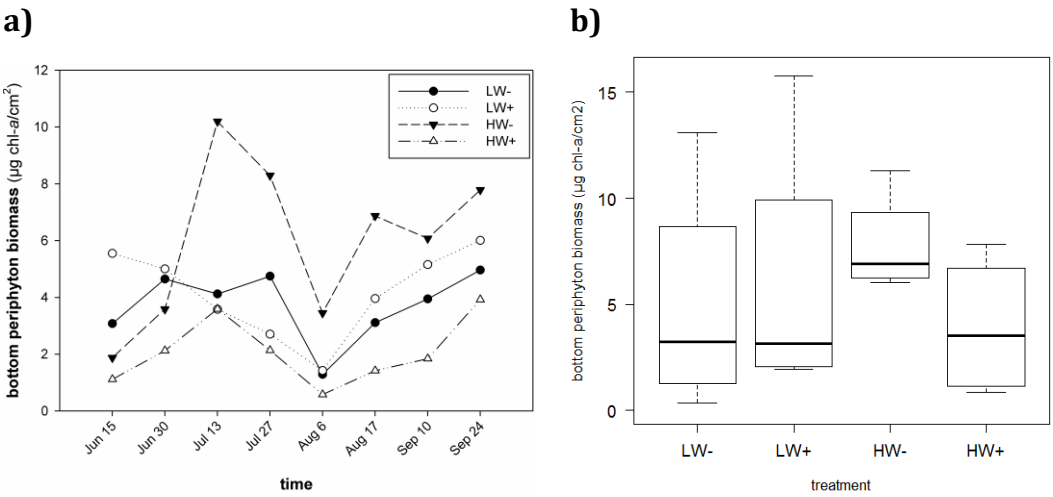

Figure 12: Bottom periphyton chl-*a* a) change over the course of the experiment, b) comparison of all treatments in the last sampling

3.3 Macroinvertebrate Assemblages

All benthic and macrophyte-associated macroinvertebrates identified in the samples are listed in the Appendix together with their taxonomic classifications, common names and functional feeding groups. A total of 15 taxa (at family level) were found in the sediment and plant samples. Specimens at different stages of their life-cycle (e.g. larvae and pupae of Diptera, nymphs of aquatic insects) in addition to adults were counted in the samples. After counting separately, specimens belonging to the same taxonomic group were summed for data analyses. Identified macroinvertebrates were grouped according to their feeding guilds mainly as predators, grazers and detritivores.

Abundance of benthic macroinvertebrates at the initial, middle and final sampling events and abundance of macrophyte-associated macroinvertebrates are given in Tables 6, 7, 8 and 9, respectively. As is evident from the tables, there was a large variation of macroinvertebrates among the treatments, even among the replicates of the same treatment. For this reason, mean count data per sample in the tables are given in decimals

(though they show the number of individuals) so as not to underrepresent rare taxa (i.e. those present only in one or few replicates with very few individuals). Taxa that were not abundant were also taken into account in the data analyses because of likelihood of high patchiness and heterogeneity of macroinvertebrate distribution.

The following parameters were chosen for defining the abundance and community composition of the macroinvertebrates:

- *Density*: For benthic macroinvertebrates, individuals found in m^2 of sediment, was calculated by dividing the total number of individuals counted in a sample by the total surface area of three sediment core samples taken by Kajak corer (internal diameter of 5.2 cm), assuming that macroinvertebrates were dwelling the surface of the sediment and not the whole core volume. For macrophyte-associated macroinvertebrates, density was defined as the number of individuals per 100 g dry plant biomass. It was calculated by dividing the total number of individuals counted in a sample by the dry weight of the macrophytes harvested from that sample.

- *Taxa richness*: Since all individuals were identified at least to family level, family level richness was taken as a basis for comparative purposes even though some individuals could be identified to lower taxonomic levels such as subfamily or genus.

- *Predator density*: Density of individuals belonging to predator groups (i.e. Ceratopogonidae, Chaoboridae, Corixidae, Coenagrionidae, Hygrobatidae, Hydrophilidae, Dytiscidae) was used as this parameter, together with the following one, could give insight into the interrelations of different functional feeding groups.

- *Grazer-detritivore density*: Density of individuals belonging to grazer (i.e. Chironomidae, Ephydridae, Baetidae, Aphididae, Planorbidae) and detritivore (i.e. Lumbricidae, Sminthuridae, Isotomidae) groups were pooled together as

the amount of detritus was expected to be higher in the treatments where substrate for grazers was available.

- *Chironomid density*: Density of Chironomidae was used to estimate the grazing pressure exerted on epiphyton and periphyton as chironomids were usually the dominant taxa among grazers.

- V*ulnerable density*: Density of individuals belonging to taxa that are vulnerable to fish predation (i.e. *Chaoborus* sp., Corixidae, Odonata and Ephemeroptera) were taken into consideration as these could be a indicative of fish presence/absence.

Table 6: Abundance (mean ± SD per sample) of benthic macroinvertebrates in all treatments at the initial sampling (Dominant taxa are highlighted by asterisks.)

Taxon	Abundance (mean ± SD)			
	LW-	LW+	HW-	HW+
Ceratopogoninae*	0.25±0.50	0.00±0.00	15.00±26.70	6.00±4.08
Chaoborus sp.	0.00±0.00	0.00±0.00	0.75±0.96	0.00±0.00
Chironomidae*	3.00±4.08	8.50±8.27	2.25±1.71	3.50±1.00
Brachycera	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Oligochaeta	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Corixidae	1.00±2.00	0.50±1.00	0.00±0.00	0.00±0.00
Coenagrionidae	0.00±0.00	1.00±0.00	0.00±0.00	0.00±0.00
Baetidae	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Hygrobatidae	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Aphididae	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00

Table 7: Abundance (mean ± SD per sample) of benthic macroinvertebrates in all treatments at the middle sampling (Dominant taxa are highlighted by asterisks.)

Taxon	Abundance (mean ± SD)			
	LW-	LW+	HW-	HW+
Ceratopogoninae*	0.00±0.00	0.25±0.50	9.75±12.45	2.25±2.63
Chaoborus sp.*	2.50±2.38	0.00±0.00	2.25±2.22	0.50±1.00
Chironomidae	1.00±1.41	0.50±0.58	1.25±1.26	0.50±1.00
Brachycera	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Oligochaeta	0.25±0.50	0.75±0.96	0.00±0.00	0.00±0.00
Corixidae*	0.50±1.00	0.25±0.50	36.00±41.86	0.00±0.00
Coenagrionidae	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Baetidae	1.50±0.71	0.00±0.00	0.00±0.00	0.00±0.00
Hygrobatidae	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Aphididae	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00

Table 8: Abundance (mean ± SD per sample) of benthic macroinvertebrates in all treatments at the final sampling (Dominant taxa are highlighted by asterisks.)

Taxon	Abundance (mean ± SD)			
	LW-	LW+	HW-	HW+
Ceratopogoninae*	5.00±5.35	5.25±4.50	13.00±14.72	0.50±1.00
Chaoborus sp.	1.75±2.87	0.25±0.50	0.25±0.50	1.00±1.15
Chironomidae	0.25±0.50	1.00±1.15	0.50±0.58	1.25±1.26
Brachycera	0.00±0.00	1.50±1.73	0.00±0.00	0.00±0.00
Oligochaeta	0.25±0.50	0.25±0.50	0.00±0.00	0.00±0.00
Corixidae*	10.25±13.72	0.75±0.96	104.75±123.2	10.25±14.61
Coenagrionidae	1.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Baetidae	0.00±0.00	3.00±0.00	0.00±0.00	0.00±0.00
Hygrobatidae	0.00±0.00	1.00±0.00	0.00±0.00	0.00±0.00
Aphididae	0.00±0.00	1.00±0.00	0.00±0.00	0.00±0.00

Table 9: Abundance (mean ± SD per sample) of macrophyte-associated macroinvertebrates in all treatments at the end of the experiment (Dominant taxa are highlighted by asterisks.)

Taxon	Abundance (mean ± SD)			
	LW-	LW+	HW-	HW+
Ceratopogoninae*	41.00±67.56	27.67±14.57	3.33±3.06	0.00±0.00
Chaoborus sp.	0.67±1.15	1.67±2.89	0.00±0.00	0.00±0.00
Chironomidae*	478.67±242.	518.33±441.	35.67±53.35	6.67±11.55
Brachycera*	57.67±87.78	28.67±4.04	0.00±0.00	0.00±0.00
Corixidae*	14.67±12.10	217.33±369.	3.67±3.51	0.00±0.00
Coenagrionidae*	31.67±32.33	103.33±94.4	0.00±0.00	0.00±0.00
Baetidae*	52.33±49.96	26.50±26.16	0.00±0.00	0.00±0.00
Coleoptera	0.33±0.58	1.67±2.89	1.67±2.08	0.00±0.00
Isotomidae	0.00±0.00	1.67±1.15	0.00±0.00	0.00±0.00
Sminthuridae	20.00±32.91	8.00±5.66	0.50±0.71	0.00±0.00
Aphididae*	10.33±12.74	458.00±790.	0.00±0.00	0.00±0.00
Planorbidae	1.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00

3.3.1 Benthic Macroinvertebrates

According to the results of one-way ANOVA for the initial sampling (Table 10), none of the parameters showed significant difference between the LW and HW mesocosms. Thus, the initial conditions regarding benthic macroinvertebrates were accepted as similar at the two different locations. The changes in all parameters in the mesocosms through the initial, middle and final sampling events are depicted in Figure 13–18.

Table 10: One-way ANOVA results showing the influence of water level on the initial sampling of benthic invertebrates (ns denotes a non-significant difference with $p>0.05$.)

Parameter	*p*
Density	ns
Taxa richness	ns
Predator density	ns
Grazer-detritivore density	ns
Chironomid density	ns
Vulnerable density	ns

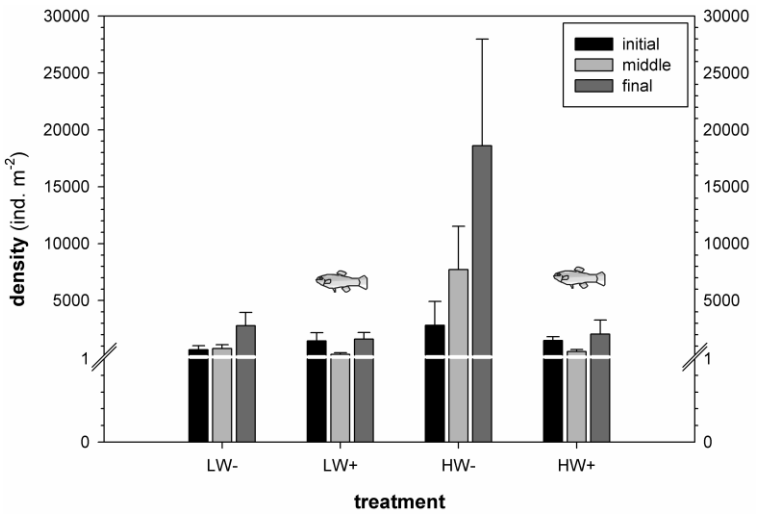

Figure 13: Change in mean (± SE) density in all treatments through the initial, middle and final sampling of benthic macroinvertebrates

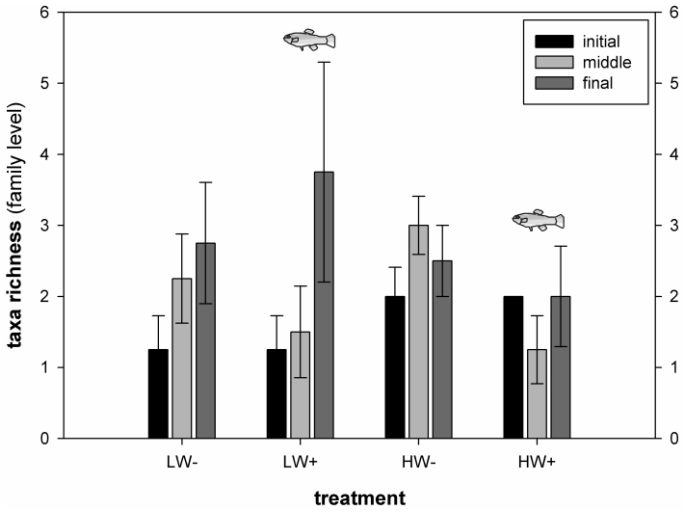

Figure 14: Change in mean (± SE) taxa richness in all treatments through the initial, middle and final sampling of benthic macroinvertebrates

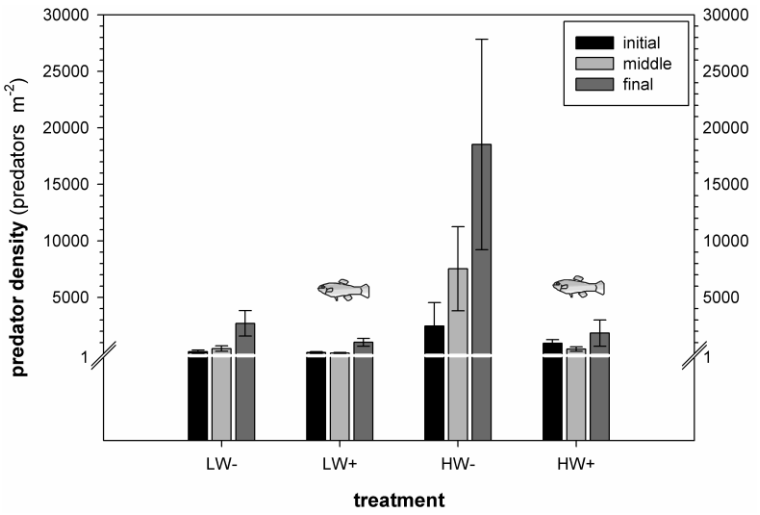

Figure 15: Change in mean (± SE) predator density in all treatments through the initial, middle and final sampling of benthic macroinvertebrates

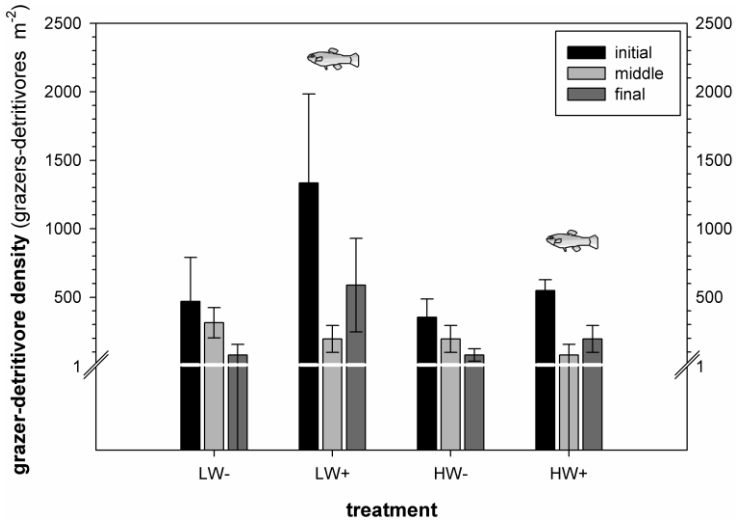

Figure 16: Change in mean (± SE) grazer-detritivore density in all treatments through the initial, middle and final sampling of benthic macroinvertebrates

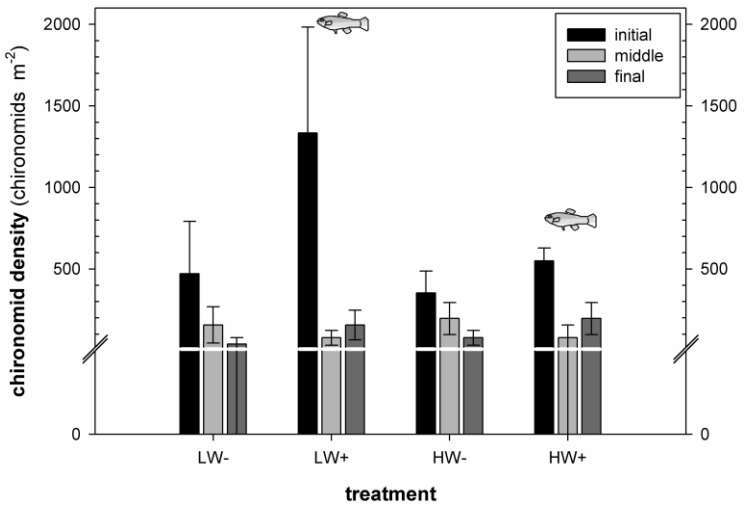

Figure 17: Change in mean (± SE) chironomid density through the initial, middle and final sampling of benthic macroinvertebrates

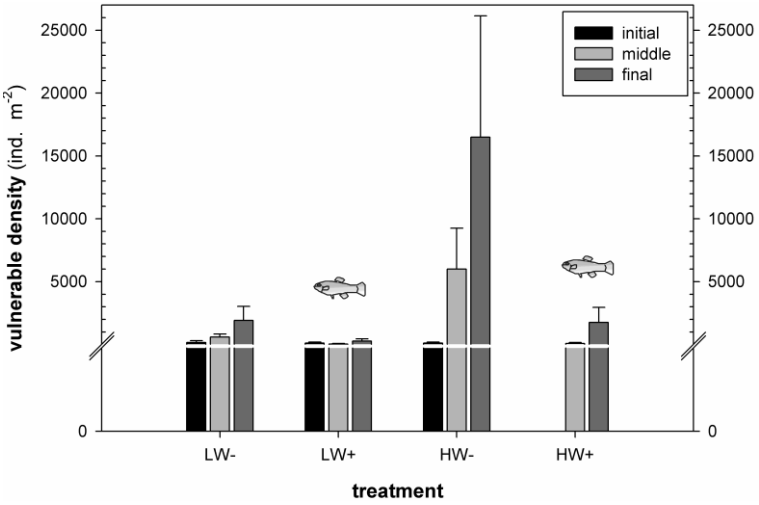

Figure 18: Change in mean (± SE) vulnerable density in all treatments through the initial, middle and final sampling of benthic macroinvertebrates

The two-way ANOVA results for the middle sampling of benthic macroinvertebrates (Table 11) indicate that there was a significant impact of fish on the density (p=0.045, Figure 19), taxa richness (p=0.042, Figure 20) and vulnerable density (p<0.001, Figure 21). None of the parameters were significantly affected by water level. Benthic macroinvertebrate density as

well as taxa richness (Tukey test between HW- and HW+ treatments, p=0.044) was significantly higher in fishless enclosures than the enclosures with fish. At both LW and HW, vulnerable density was significantly lower in the mesocosms with fish than fishless mesocosms (Tukey test; p=0.01 and p=0.002, respectively).

Table 11: Two-way ANOVA results showing the influence of water level, fish and their interaction on the middle sampling of benthic macroinvertebrates (ns denotes a non-significant difference with $p > 0.05$.)

Parameter	*p*		
	WL	**F**	**WL*F**
Density	ns	0.045	ns
Taxa richness	ns	0.042	ns
Predator density	ns	ns	ns
Grazer-detritivore density	ns	ns	ns
Chironomid density	ns	ns	ns
Vulnerable density	ns	<0.001	ns

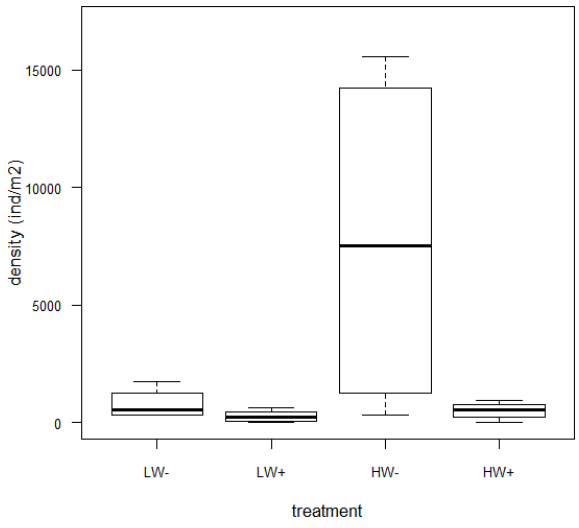

Figure 19: Density of benthic macroinvertebrates in all treatments in the middle sampling

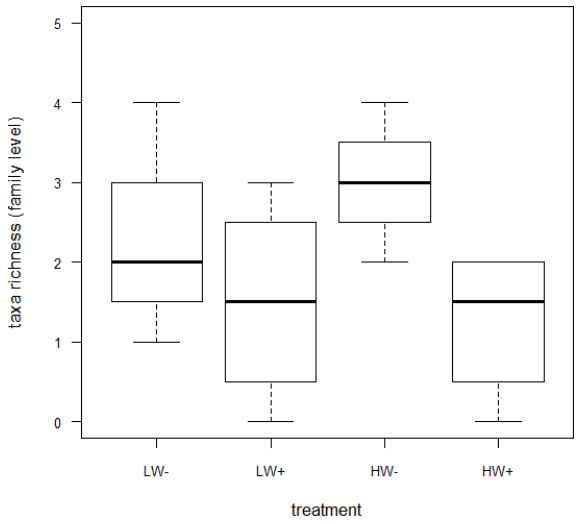

Figure 20: Taxa richness of benthic macroinvertebrates in all treatments in the middle sampling

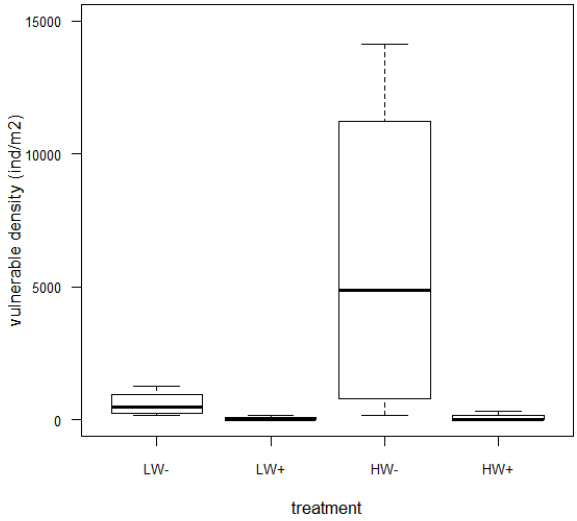

Figure 21: Vulnerable density of benthic macroinvertebrates in all treatments in the middle sampling

The two-way ANOVA results for the final sampling of benthic macroinvertebrates (Table 12) show that there was a significant effect of fish only on the predator density (p=0.049, Figure 22), as it was significantly lower in the mesocosms with fish than fishless mesocosms at both LW and

HW (Tukey test; p=0.049 and p=0.024, respectively). None of the parameters were significantly affected by water level.

Table 12: Two-way ANOVA results showing the influence of water level, fish and their interaction on the final sampling of benthic macroinvertebrates (ns denotes a non-significant difference with $p > 0.05$.)

Parameter	*p*		
	WL	**F**	**WL*F**
Density	ns	ns	ns
Taxa richness	ns	ns	ns
Predator density	ns	0.049	ns
Grazer-detritivore density	ns	ns	ns
Chironomid density	ns	ns	ns
Vulnerable density	ns	ns	ns

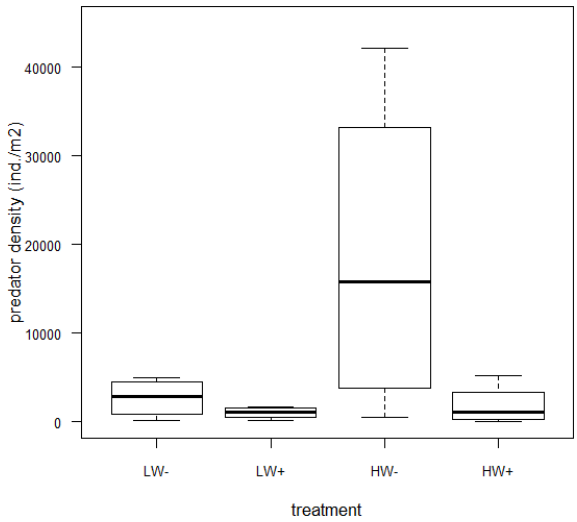

Figure 22: Predator density of benthic macroinvertebrates in all treatments in the final sampling

3.3.2 Macrophyte-associated Macroinvertebrates

The two-way ANOVA results for macrophyte-associated macroinvertebrates (Table 13) indicate that there was a significant impact of water level on the

taxa richness (p<0.001) predator density (p=0.004) and vulnerable density (p=0.004). None of the parameters were significantly affected by fish presence/absence. The comparison of the parameters across all treatments is demonstrated by box-plots in Figure 23. Taxa richness was significantly higher in LW- enclosures than HW- enclosures, and in LW+ enclosures than HW+ enclosures (Tukey test, p<0.001 for both). HW- treatments had the highest predator and vulnerable density.

Table 13: Two-way ANOVA results showing the influence of water level, fish and their interaction on the macrophyte-associated macroinvertebrates (ns denotes a non-significant difference with $p > 0.05$.)

Parameter	*p*		
	WL	**F**	**WL*F**
Density	ns	ns	ns
Taxa richness	<0.001	ns	ns
Predator density	0.004	ns	ns
Grazer-detritivore density	ns	ns	ns
Chironomid density	ns	ns	ns
Vulnerable density	0.004	ns	ns

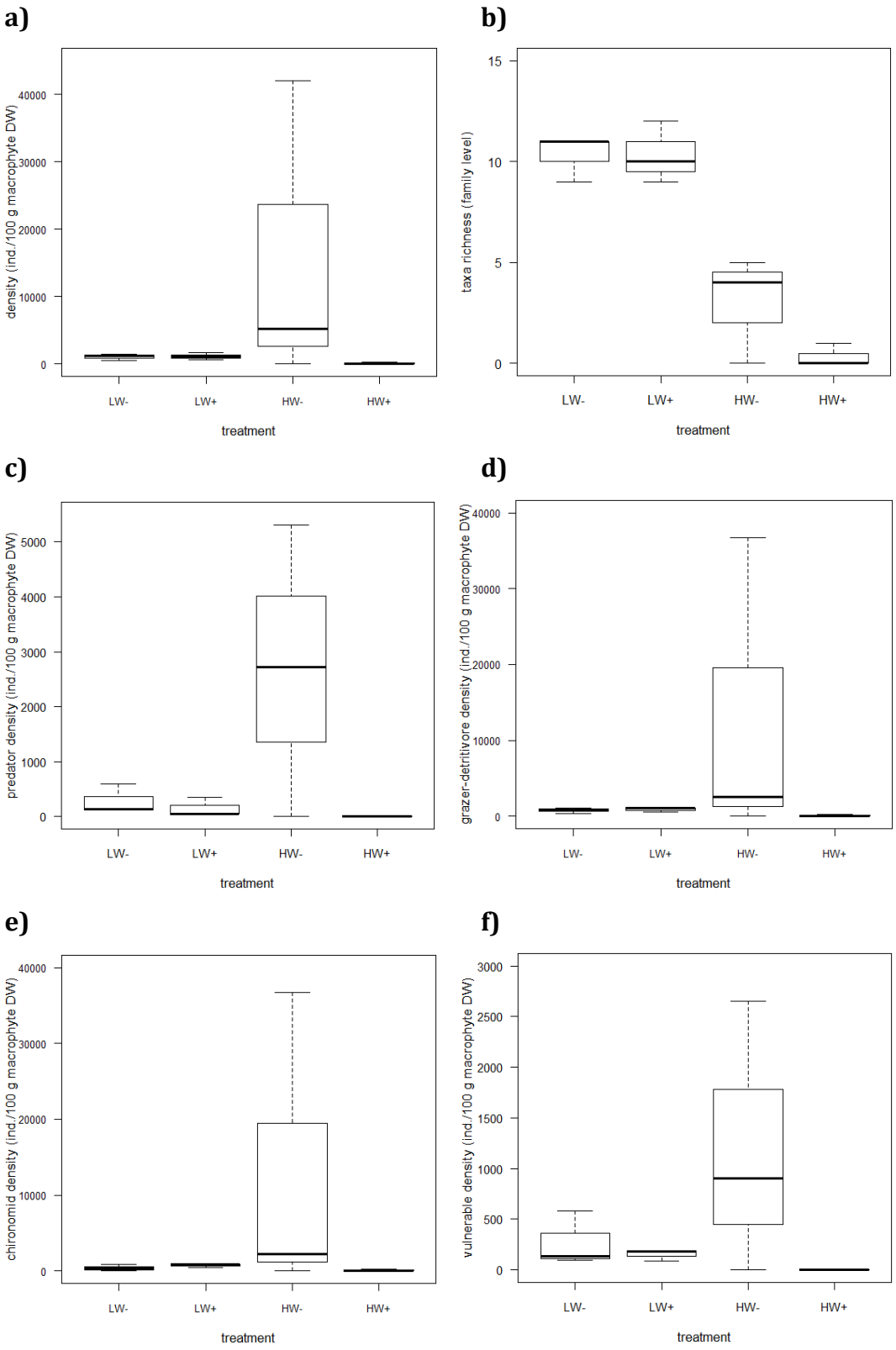

Figure 23: Comparison of the parameters for macrophyte-associated macroinvertebrates in all treatments a) total density, b) taxa richness (family level), c) predator density, d) grazer-detritivore density, e) chironomid density, f) vulnerable density

CHAPTER 4

DISCUSSION & CONCLUSION

4.1 Discussion

Following the study of Özkan (2008), the mesocosm experiment was conducted with the purpose of determining the effects of water level fluctuations and fish predation on submerged macrophyte growth in a semi-arid shallow eutrophic lake. Submerged plant development being the main focus of the experiment and the subject of another thesis, its relationship with physico-chemical variables and nutrient availability under the influence of water level change and fish presence were thoroughly discussed by Bucak (2011).

With this thesis, the relative influences of top-down and bottom-up interactions on periphyton growth and macroinvertebrates were aimed to be investigated by manipulating fish presence at different water levels in the *in situ* mesocosms. Thus, the focus of discussion is on macroinvertebrates in relation to fish predation and periphyton growth brought about by change in water levels.

In the summer of 2009, when the experiment was carried out, frequent rain events were experienced in the first few weeks of June, while temperature rise became more apparent as from July. This led to increased evaporation and a corresponding drop of water levels. At the end of the 4-month sampling

period, the water level had decreased by an average of 0.46 ± 0.03 m (Figure 7), which is characteristic of the Mediterranean semi-arid climate.

The Secchi disc depth/average depth ratio in the mesocosms differed significantly under the influence of water level and fish. Underwater light penetration was higher in the fishless enclosures over the course of the experiment. Water clarity was higher in LW enclosures and phytoplankton biomass was lower in the fishless enclosures at the end of the experiment. The highest Secchi disc depth/average depth ratio was observed in the LW- treatment (Figure 8).

Both water level and fish had a significant impact on submerged macrophytes. Macrophyte development occurred in the LW enclosures despite having had high concentrations of N and P, but not in the HW enclosures. Dry weight of macrophytes and %PVI were both found to be higher in LW- than LW+ enclosures at the end of the experiment (Figure 9). Plant growth remained very low in HW- enclosures despite high water clarity, which may be the result of competition with periphyton for light in the lower part of the water column (Bucak, 2011).

In accordance with previous studies (Coops et al., 2005; Beklioglu et al. 2006; Özkan et al., 2010) which suggest that water level is critical for macrophyte development in semi-arid climatic regions, Bucak (2011) has concluded that low water levels during growth season might override the adverse effects of eutrophication and intense top-down control of fish, and allow macrophyte growth even under poor light availability in the water column.

4.1.1 Epiphyton and Periphyton

The highest epiphyton chl-*a* was observed in HW- enclosures (Figure 10). The inverse correlation between invertebrate grazers and epiphyton has been well documented by exclosure-enclosure and large-scale experiments

(Cattaneo, 1983; Jones et al., 2002; Jones & Sayer, 2003). Since HW- enclosures had significantly higher predator macroinvertebrate density than LW- enclosures at the end of the experiment (Figure 23), there is evidence to suggest that grazing pressure on epiphyton exerted by grazers was reduced and top-down control of predators on grazers favoured the growth of epiphyton.

While upper periphyton chl-*a* did not vary significantly among treatments, bottom periphyton chl-*a* was significantly affected by both water level and fish. Negligible variation in the upper periphyton biomass among treatments can be expected since underwater light attenuation might be constant in the upper part of the water column close to the lake surface, regardless of water clarity and treatment effects.

As in the case of epiphyton, HW- enclosures had the highest bottom periphyton biomass (Figure 12). It seems likely that periphyton took advantage of the high water clarity in HW- enclosures favourable for growth and succeeded in the competition with macrophytes. In agreement with Williams et al. (2002), macrophyte growth was halted as a result of shading by periphyton. Moreover, increasing density of benthic and macrophyte-associated predator macroinvertebrates in HW- enclosures might have inhibited periphyton grazing.

In the LW mesocosms, LW+ treatments had higher bottom periphyton biomass than LW- treatments. It is possible that macrophytes succeeded in the competition for light and dense macrophyte beds in LW- enclosures caused a reduction in periphyton growth by shading in this case. This pattern also coincides with the results of a previous enclosure experiment which showed that the presence of fish had directly or indirectly a positive effect on the periphyton biomass (Liboriussen et al., 2005).

4.1.2 Macroinvertebrates

Highly variable distribution and abundance of several taxa in the enclosures implied the patchy and heterogeneous existence of macroinvertebrates in lentic ecosystems (Baumgärtner et al., 2008). For instance, large number of individuals of a taxon was counted in a replicate while none or very few individuals belonging to the same taxon were encountered in another replicate of even the same treatment. Also, it was common to count only a few individuals of a taxon in a single replicate among all treatments (see Table 6-Table 9 for raw data). Detecting changes in the fauna requires extensive efforts to obtain sufficient statistical data (Baumgärtner et al., 2008), so the macroinvertebrate analysis results in the previous chapter should be interpreted cautiously. The following discussion on macroinvertebrates was based on the statistical analysis results as well as the comparison of count data in order to see more clearly the trends that were not explicit in statistical analyses.

Initial sampling of benthic macroinvertebrates revealed no significant difference between the LW and HW mesocosms. Similarity of the initial conditions at these two distant locations were expected since the sediment characteristics (LOI results for organic matter and carbonate content estimation) were also similar for both LW and HW mesocosms, and the lake bottom was cleared of vegetation prior to the placement of the mesocosms.

Fish had a significant effect on total density, taxa richness and vulnerable density in the middle sampling (Table 11), and on predator density in the final sampling (Table 12) of benthic macroinvertebrates. Water level had no significant impact on any of the parameters in either sampling events. The trends evident between the two consecutive sampling events (i.e. effect of time) did not prove to be statistically significant.

The density of benthic macroinvertebrates was highest in HW- enclosures (Figure 13). Fish-free enclosures had higher density than the enclosures with

fish. Benthic macroinvertebrate density remained lower in treatments with fish throughout the experiment as a result of top-down control of fish. Though not statistically significant, macroinvertebrate densities showed a continuously increasing trend in fish-free enclosures over the course of the experiment whereas a downward unimodal (decreasing and then increasing) trend was observed in the enclosures with fish. The reason for this may be the high predation pressure of fish on bare sediment, but in time the predation pressure might have been diminished by the growth of submerged macrophytes and their refuge effect.

Fish had a statistically significant impact on taxa richness in the middle sampling, but not in the final sampling of benthic macroinvertebrates. Taxa richness was highest in HW- enclosures and higher in fishless treatments in the middle sampling (Figure 20). But at the end of the experiment, this difference disappeared and richness increased in LW treatments likely as a result of the extensive macrophyte coverage in both LW- and LW+ enclosures.

Fish had a significant effect on predator density only in the final sampling of benthic macroinvertebrates. Predator density was highest in HW- treatments and had an obviously increasing trend in the fish-free enclosures throughout the experiment (Figure 15). On the contrary, grazer-detritivore density decreased in these enclosures where predators increased in abundance (Figure 16). A similar trend in chironomid density was apparent in fishless enclosures (Figure 18) as Chironomidae was the most abundant taxon within the grazer-detritivore group. These results support the evidence that large, predatory invertebrates are capable of reducing density of their prey (Diehl, 1992; Prejs et al., 1997). The contrasting patterns in the densities of predators and grazer-detritivores suggest that, in the absence of fish, internal predation dynamics of macroinvertebrates can be as important in influencing their community structure as fish predation pressure. Moreover, cascading top-down effects may have implications for epiphyton and periphyton, as discussed in the previous section.

The density of vulnerable taxa was significantly influenced by fish in the middle sampling (Figure 21), but not in the final sampling of benthic macroinvertebrates. It was higher in the fishless enclosures and had an increasing trend throughout the experiment (Figure 18). The highest vulnerable density was observed in HW- enclosures. Data revealed that individuals of taxa known to be vulnerable to fish predation (e.g. *Chaoborus* larvae and Corixidae) were more abundant in the mesocosms without fish, whereas they were rare or absent in the fishless mesocosms (see Table 6-Table 9 for raw data), indicating that the exclusion of fish from the system possibly led to an increase in the density of these taxa. This result is in agreement with Eriksson et al. (1980), who documented that taxa suppressed by fish predation becomes abundant when fish predation ceases. In addition to the direct effect of fish predation, exclusion of these large-size selective predators from the system can also have implications for altering community composition via replacement of fish by such small-size selective predators and other aquatic insects, and a consequent shift to invertebrate-dominated predator-prey systems (Eriksson et al., 1980).

On the other hand, fish did not have any statistically significant effect on macrophyte-associated macroinvertebrates while taxa richness, density of predators and vulnerable taxa were significantly influenced by water level (Table 13).

In LW enclosures where extensive submerged plant growth was observed, taxa richness of macrophyte-associated macroinvertebrates was significantly higher than HW mesocosms (Figure 23). On the other hand, a common pattern was observed for all density-related parameters: HW- enclosures had the highest densities of macrophyte-associated macroinvertebrates whereas densities in LW- and LW+ enclosures were similar but lower as compared to HW- enclosures. Within the treatments containing fish, LW enclosures had significantly higher density of predators and vulnerable taxa than HW enclosures. Taking into consideration the difference in %PVI among LW and

HW mesocosms at the end of the experiment (Figure 9), it is likely that the dense macrophyte stands in LW enclosures contributed more to richness than the sparse vegetation in HW enclosures. Moreover, similar macroinvertebrate densities among LW- and LW+ enclosures suggest that the impact of fish predation became insignificant in dense vegetation whereas fish could still forage for the large-size predators and vulnerable taxa among sparse macrophyte stands.

The pronounced top-down influence of fish on benthic macroinvertebrates is consistent with the results of several other experimental studies investigating the effects of fish predation (Diehl, 1992; Diehl & Kornijów, 1998; Jones et al., 2002; Williams et al., 2002; Leppä et al., 2003; Beresford & Jones, 2010). Moreover, the patterns within predator and grazer macroinvertebrates partly coincide with a previous study (Prejs et al., 1997) which suggested an important control of macroinvertebrate predators on their prey once suppression by fish was released.

Dense macrophyte growth was observed in LW enclosures with the reduction in water level towards the end of the experiment period. As conceptualized in Figure 24, indirect effects on WLF on macroinvertebrates became apparent in time as PVI increased. In accordance with previous studies which showed that submerged vegetation can diminish or eliminate the top–down effects of fish on macroinvertebrates via providing a refuge (Gilinsky, 1984), creating habitat complexity and reducing the foraging efficiency of fish (Crowder & Cooper, 1982; Diehl, 1992), fish predation pressure was diminished in LW mesocoms.

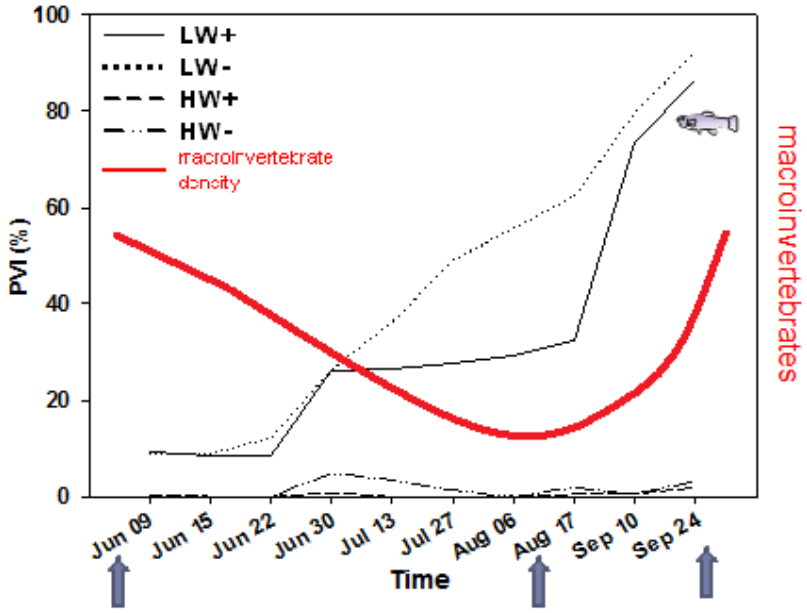

Figure 24: Conceptual response of macroinvertebrates to macrophyte growth by decreasing water levels (Blue arrows indicate sampling dates.)

Comparison of the parameters across macrophyte-associated macroinvertebrates and final sampling of benthic macroinvertebrates revealed that the patterns generally coincided. For instance, HW- enclosures had higher predator and vulnerable densities and lower grazer-detritivore and chironomid densities of both macrophyte-associated and benthic macroinvertebrates. Thus, there is evidence to suggest that benthic and macrophyte-associated macroinvertebrates were closely interacting and presence of submerged macrophytes sustained both communities.

4.2 Conclusion

The aim of this study was to demonstrate the relative influences of top-down and bottom-up forces on periphyton growth and macroinvertebrate community structure by manipulating fish presence at different water levels in the *in situ* mesocosms. We hypothesised that macroinvertebrate community structure would be adversely affected by fish predation whereas a

decline in water level and a corresponding macrophyte growth and periphyton development would favor macroinvertebrates even at presence of fish.

Though large variation of macroinvertebrate count data in replicate samples and presence of very few individuals from some taxa created complicated the interpretation of the results, examination of raw data gave insight to the possible relations. Evidence was obtained to suggest that fish predation pressure may have significant influence on macroinvertebrate communities in terms of both abundance and richness in the absence of vegetation. Stronger predator-prey interaction among macroinvertebrate community in the absence of fish was apparent from the replacement of fish suppression by predator macroinvertebrates.

No direct effect of water depth on macroinvertebrate community structure seemed to be evident. However, as observed in this mesocosm experiment, water level fluctuations may have an overriding impact on the growth of submerged macrophytes in semi-arid shallow lakes. In turn, structural complexity created by dense vegetation may weaken the top-down effect of fish on macroinvertebrates by acting as a refuge. This interaction constitutes an indirect way by which water level fluctuations affect macroinvertebrate community structure. Despite their weakened role as refuge and fish omnivory in semi-arid regions, macrophytes seem to be critical in sustaining macroinvertebrate communities in the light of the evident impacts of climate change on freshwater ecosystems.

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Taxonomical classification, feeding group and common name of benthic macroinvertebrates
(Most abundant taxa are denoted by asterisks.)

Taxonomic level	Macroinvertebrates identified										
Domain	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota
Kingdom	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia
Phylum	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Annelida	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda
Class	Insecta	Insecta	Insecta	Insecta	Insecta	Clitellata	Insecta	Insecta	Insecta	Arachnida	Insecta
Subclass						**Oligochaeta**	Dicondylia	Dicondylia	Pterygota	Acari	
Superorder										Acariformes	
Order	Diptera	Diptera	Diptera	Diptera	Ephemeroptera	Haplotaxida	Hemiptera	Hemiptera	Odonata	Actinedida	Hemiptera
Suborder				Brachycera			Heteroptera	Heteroptera	Zygoptera	Parasitengona	**Sternorrhyncha**
Infraorder							Nepomorpha	Nepomorpha			
Superfamily				Ephydroidea						Hygrobatoidea	Aphidoidea
Family	Ceratopogonidae	Chaoboridae	**Chironomidae***	**Ephydridae**	**Baetidae***	**Lumbricidae**	Corixidae	Corixidae	**Coenagrionidae**	**Hygrobatidae**	**Aphididae**
Subfamily	**Ceratopogoninae***		Chironominae				**Micronectinae**	**Corixinae**			
Tribe			**Chironomini**								
Genus		**Chaoborus**	**Chironomus***		**Cloeon**	**Eiseniella**					
common name	biting midge	phantom mid	non-biting midge	shore fly	mayfly	aquatic earthv	water boatman	water boatma	damselfly	water mite	aphid
feeding group	predator	predator	grazer	grazer	grazer	detritivorous	predator	predator	predator	predator	grazer

Taxonomical classification, feeding group and common name of macrophyte-associated macroinvertebrates (Most abundant taxa are denoted by asterisks.)

Taxonomic level	Macroinvertebrates identified													
Domain	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota	Eukaryota
Kingdom	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia	Animalia
Phylum	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Arthropoda	Mollusca
Class	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Insecta	Entognatha	Entognatha	Insecta	Gastropoda
Subclass						Dicondylia	Dicondylia	Pterygota	Coleoptera	Coleoptera	Collembola	Collembola		
Superorder									Staphyliniformia					
Order	Diptera	Diptera	Diptera	Diptera	Ephemeroptera	Hemiptera	Hemiptera	Odonata			Symphypleona	Entomobryomorpha	Hemiptera	
Suborder				Brachycera		Heteroptera	Heteroptera	Zygoptera					**Sternorrhyncha**	
Infraorder						Nepomorpha	Nepomorpha							
Superfamily				Ephydroidea					Hydrophiloidea	Dytiscoidea			Aphidoidea	Planorboidea
Family	Ceratopogonidae	Chaoboridae	**Chironomidae***	**Ephydridae**	**Baetidae***	Corixidae	Corixidae	**Coenagrionidae**	**Hydrophilidae**	**Dytiscidae**	**Sminthuridae**	**Isotomidae**	**Aphididae***	**Planorbidae**
Subfamily	**Ceratopogoninae***		Chironominae			**Micronectinae***	**Corixinae**							
Tribe			**Chironomini**											
Genus		**Chaoborus**	**Chironomus***		**Cloeon**									
common name	biting midge	phantom midge	non-biting midge	shore fly	mayfly	water boatman	water boatman	damselfly	water scavenger	predaceous	globular springt	springtail	aphid	ramshorn snail
feeding group	predator	predator	grazer	grazer	grazer	predator	predator	predator	predator	predator	detritivorous	detritivorous	grazer	grazer