ZOOPLANKTON ADAPTATION STRATEGIES AGAINST FISH PREDATION IN TURKISH SHALLOW LAKES

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ABSTRACT

ZOOPLANKTON ADAPTATION STRATEGIES AGAINST FISH PREDATION IN TURKISH SHALLOW LAKES

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In this study, the factors influencing zooplankton community structure in Turkish shallow lakes were elucidated with four main approaches: (i) space-for-time substitution for shallow lakes using snap-shot sampling in 31 lakes along a latitudinal gradient; (ii) *in-situ* mesocosm experiments in eleven lakes along a latitudinal gradient using three sets of artificial plants systems; (iii)'Habitat Choice' laboratory experiments mimicking a 'shallow littoral' zone with plants and a 'deeper pelagic' zone with sediments testing the response of *Daphnia magna* to predation cues; and (iv) long-term monitoring data (1997-2011) from two interconnected lakes.

Snap-shot and long-term monitoring showed that eutrophication has a strong influence on the zooplankton community via increased fish predation, nutrient loading and salinization. Here too the zooplankton community shifted towards a smaller sized profile, especially in lakes located at lower latitudes. Moreover, The laboratory and *in-situ* mesocosm experiments revealed that under predation risk *Daphnia* preferred to hide near sediment instead of using submerged plants as a refuge. Accordingly, *in-situ* mesocosm experiments revealed a predation pressure induced size structure shift towards small-medium sized zooplankton and calanoid copepods.

The long-term monitored lakes experienced (i) drought-induced water level drop, leading to increased salinity and eutrophication, and consequent anoxic conditions and fish kill; as well as (ii) biomanipulation in the downstream. Both conditions resulted in major reduction in the top-down control of fish and ultimate predomination by large sized *Daphnia* spp.

Nevertheless, the excessive exploitation of lakes and ongoing warming entail Turkish shallow lakes to become more eutrophic, making this study indicative for the Mediterranean region.

Keywords: diel vertical/horizontal migration, size structure, water level changes, salinity, biomanipulation

ÖZ

TÜRKİYE SIĞ GÖLLERİNDE BALIK AVLANMA BASKISI KARŞISINDA ZOOPLANKTONUN UYUM STRATEJİLERİ

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Bu tezde, Türkiye'de bulunan sığ göllerdeki zooplankton komünite yapısını etkileyen etmenler dört ana yaklaşım kullanılarak açıklanmıştır: (i) enlemsel hat botunca 31 sığ gölün zaman yerine mekan yaklaşımı kullanılarak anlık fotoğraf çekme yöntemi ile örneklenmesi;(ii) enlemsel hat boyunca onbir gölde üçer set yapay bitki düzeneği kullanılarak gerçekleştirilen yerinde (*in-situ*) mezokozm deneyleri; (iii) 'Habitat tercihi' laboratuvar deneyleri bitki kullanılarak 'sığ littoral' bölgenin ve çökel kullanılarak 'derin pelajik' bölgenin taklit edilmesi ile *Daphnia magna'* nın avcı sinyali karşısında vereceği tepki test edilmiştir; ve (iv) birbirine bağlı iki gölde yapılan uzun dönemli (1997-2011) izleme çalışması.

Anlık fotoğraf çekme örneklemesi ve uzun dönemli izleme çalışmasına göre ötrofikasyonun balık avlanma baskısı, besin tuzu yüklemesi ve tuzlanmaya bağlı olarak zooplankton toplulukları üzerinde etkili olduğunu göstermiştir. Aynı şekilde düşük enlemlerdeki göllerde küçük vücutlu zooplankton türlerinin baskın olmasına neden olduğu tespit edilmiştir. Laboratuvar ve yerinde mezokozm deneyleri avlanma riski karşısında *Daphnia*'nın suiçi bitkiler yerine çökeli barınak olarak tercih ettiğini göstermiştir. Ayrıca yerinde mezokozm deneyleri avlanma baskısı karşısında zooplanktonun küçük-orta büyüklükteki türler ile calanoid copepod' a doğru değiştiğini göstermiştir.

İzleme çalışmasına göre göller (i) kuraklığa bağlı olarak meydana gelen su seviyesi düşmesi ile tuzluluğun artmasını ve ötrofikasyonu tetiklemiştir ve bunların sonucunda anoksik koşullar ve balık ölümleri ile; (ii) althavzada biyomanipulasyon etkisi altındadır. Bu koşullar balığın yukardan-aşağı kontrolünü azaltarak büyük vücutlu türlerin özellikle *Daphnia* spp. 'ın baskın duruma geçtiğini göstermiştir.

Ancak göllerin aşırı kullanımı ve süregelen ısınma Türkiye'de bulunan sığ göllerin giderek daha ötrofik olmasına neden olması bu çalışmanın Akdeniz ikliminin hakim olduğu bölgelerdeki göller için belirleyici olabilir.

Anahtar Kelimeler: yatay/dikey göç, boy dağılım yapısı, su seviyesi değişimleri, tuzlanma, biyomanipulasyon

To scientist mothers

and

their children who are always waiting

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I believe that “only science can lead us in our life”. However, this adventure of science would have been impossible without the people in my life.

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CHAPTER 1

INTRODUCTION

1.1. Zooplankton in Shallow Lakes

Zooplankton, name was derived from Greek '*zoon*' meaning 'animal' and '*planktos*' meaning 'drifter', are organisms drifting in the water column of oceans, seas and bodies of freshwater. Planktonic organisms are mostly dominated by three major groups that are rotifers and the subclasses of Crustacea, the Cladocera and Copepoda (Wetzel, 1983). Among these groups Cladocera such as big size *Daphnia* has a crucial role in aquatic systems due to their filtration ability on phytoplankton (Moss, 1998) as well as a food source of planktivorous and omnivorous fish (Jeppesen et al., 1997). The relationship between phytoplankton and zooplankton is an important link in the food web of shallow lakes (Abrantes et al., 2006).

Top-down control of zooplankton via grazing of phytoplankton create clear water conditions with the dominance of submerged macrophyte on the other hand bottom-up forces, high nutrient loading, may responsible for the phytoplankton increase hence competition among primary producers along a nutrient gradient create two different conditions either clear water state or turbid water state that lessen the macrophyte abundance (Scheffer et al., 1993). Maintenance of clear water state, macrophytes play central role with their own stabilizing mechanisms such as: reduction of inorganic nutrient concentration from the water column thus competes for nutrients with phytoplankton (Van Donk and Van de Bund, 2002). On the other hand submerged macrophytes inhibited phytoplankton growth by secreting chemical cue (Wium-Anderson et al., 1982) though allelopathic interactions *in situ* are still missing (Mulderij et al., 2006; Gross et al., 2007).

Due to high photosynthetic activity within the macrophyte bed, may enhance the phosphorus release through sediment (Søndergaard et al., 2003). Moreover they reduce the sediment resuspension (Weisner et al., 1997).

Larger surface area of submerged macrophytes also encourages the nitrogen loss by denitrification (Weisner et al., 1994). The most important role of stabilizing effects of submerged macrophytes on water clearance in euthrophic freshwater lakes is providing daytime refuge for cladocerans (Lauridsen et al., 1996, Scheffer, 1999). Furthermore presence of piscivorous fish creates predation pressure on planktivorous thus submerged plant provide spawning habitat and refuge for them as well as zooplankton (Persson and Eklöv, 1995; Genkai-Kato, 2007). The positive impacts of submerged macrophytes on water transparency and biodiversity has recorded for many temperate lakes (Declerck et al., 2005) however in low latitudes the impacts of submerged plant seems to disappear as Bachmann et al., (2002) observed that there was no direct relation between macrophyte abundance and water transparency in subtropical Florida lakes unlike temperate shallow lakes. Furthermore, the appearance of submerged macropythes during low water level does not lead to water clarity in semi-arid Mediterranean region (Bucak et al., 2012). Therefore, aggregation of fishes within the macrophyte bed influences the predator-prey interactions (Meerhoff et al., 2003). On the other hand in Mediterranean shallow lakes, in between (sub)tropic and temperate, different ecological functions have seen due to extreme seasonality (Alverez Cobelas et al., 2005) concomitantly the zooplankton community composition is also different and mostly composed of small-size individuals because of high predation pressure (Beklioglu et al., 2003; Romo et al., 2004). Under predation pressure prey may show different morphologic, physiologic and behavioural adaptations.

1.2. Influencing Factors on Zooplankton Community

1.2.1. Hydrology

Hydrological changes which can determine by variation in precipitation, lake morphology and anthropogenic factors have catastrophic impact on shallow lakes. Semi-arid Mediterranean climatic region characterized by intra- and interannual variations in precipitation regime (Coops et al., 2003; Alvarez-Cobelas et al., 2005). Furthermore, due to high evaporation during summer, lakes are experience desiccation. Meanwhile, low water level may increase development and colonization of plant owing to increase light environment (Beklioğlu et al., 2006; Havens et al., 2007) whereas high water diminish the light reaching up to the lake bottom. Furthermore, together with the high temperature and evaporation resulting nutrient enrichment as well as salinity increased at low water level (Coops et al., 2004; Beklioğlu et al., 2007; Özen et al., 2010). Accordingly, trophic dynamics of lakes may change through dominancy of small planktivorous fish creating intense predation pressure on zooplankton (Havens et al., 2007; Jeppesen et al., 2010a; Brucet et al., 2010; Beklioğlu et al., in prep.). Thus zooplankton communities shift from large and efficient grazer to small sized individuals and copepods under high predation pressure (Beklioğlu et al., 2007; Brucet et al., 2010; Havens & Beaver, 2011). As a consequences of lowered grazing on phytoplankton induced dominancy of phytoplankton taxa such as cyanobacteria (Attayde & Hansson, 2001; Jeppesen et al., 2009; Paerl and Huisman, 2009). Despite, low water level can promote submerged plant growth, plant did not lead clear water as observed in temperate lake owing to the increased nutrient concentration and fish mediated top-down control (Bucak et al., 2012).

1.2.2. Salinity

There are several ways entering salt to aquatic environment via groundwater, weathering of rocks or from atmosphere through transported by wind and rain (Williams, 1987). The amplitude of the contribution from these sources depends on the distance from inland, climatic oscillation and geological formation (Williams, 1987).

Evaporation induced salinity increase in lakes particularly in semi-arid climates which characterized large variation in water level as a result of precipitation oscillation and dis/recharge of groundwater (Beklioğlu et al., 2007; Beklioğlu & Tan, 2008; Özen et al., 2010). Salinity changes may direct and indirect effects on freshwater biota (Nielsen et al., 2003) particularly for zooplankton the survival, abundance and reproduction are negatively influence such as delayed maturity, smaller size at first reproduction and decreased growth rate (Williams, 1987; Hart et al., 1991; Schuytema et al., 1997; Grzesiun & Mikulski, 2006; Sarma & Nandini, 2006; Bezirci et al., 2012). Furthermore, with increase in salinity resulting shift from dominance of large sized cladocerans to dominance of copepods and small sized individuals (Jeppesen et al. 2007a; Brucet et al. 2009; Jensen et al. 2010). In addition, fish assemblages may also changed along salinity increase (Jensen et al., 2010) as consisting of small planktivorous fish which have several cohorts per year (Jeppesen et al., 2007) thus effective grazers can remove (Gyllström et al., 2005; Brucet et al., 2010; 2012).

Furthermore, salinity above 0.5‰ may limit the survival of cladocerans (Jeppesen et al., 1994). Moreover, ongoing climate warming may result many freshwater lakes turn into saline in Mediterranean region (Jeppesen et al., 2009) whereby cause to changes in trophic structure in shallow lakes (Brucet et al., 2009, 2010; Jeppesen et al., 1994, 2007).

1.2.3. Predation

Among different local factors such as lake area, primary production, lake depth, nutrients, latitude, predations have important effects (Cottenie and De Meester, 2003). Different predator creates different selective forces thus predation is an important evolutionary force (Lass and Spaak, 2003; Stibor, 1992). Predators mostly feed on size-selectively and the predation strategy of predators is variable. For instance planktivorous fish hunt visually and prefer larger *Daphnia* (Lass and Spaak, 2003) hence predation of fish influence the zooplankton community composition and size of zooplankton community (Brooks and Dodson, 1965) whereas larvae of the phantom midge *Chaborous* are tactile and prefer smaller *Daphnia* (Lass and Spaak, 2003). In addition fish fry have strong impact on zooplankton during summer while they reproduce (Luecke et al., 1990; Schou et al., 2009).

Thus fish density could lead the migrating species and size classes (Jeppesen et al., 1997) that an average small size is a sign of high predation pressure (Beklioğlu & Moss, 1996; Schou et. al., 2009).

Also fish may affect the predator-prey relations in all habitats (Vander Zanden and Vadeboncoeur, 2002) such as leading to water turbidity via predation on zooplankton grazers in pelagic zone (Carpenter and Kitchell, 1993) in contrast consume macroinvertebrate grazers may lead to the out-shading of submerged macrophytes by improve periphyton growth (John and Sayer, 2003). So, spatial heterogeneity is very important in the coexistence of species (Scheffer et al., 2003). In addition, dominance of invertebrate predator influences the phytoplankton biomass.

Cladocerans are universal prey for the invertebrate as well as vertebrate predators in contrast to rotifers and copepods. Rotifers are relatively small in size. Moreover copepods are excellent swimmer hence this enables them to protect their predator (Dumont and Negrea, 2002).

However fish select for cyclopoids over calanoid copepods in the absence of *Daphnia* during autumn and winter (Bramm et al., 2009). Encounter rate depends on the distance and swimming speeds between predator and prey (Dodson, 1996). Moreover swarm formation for avoiding predation by confusion and/or dilution is very important in predator-prey interactions. But rapid consume of food is a cost within the swarm (Kvam and Kleiven, 1995). However presence of other predator in the system may force predator to change their lethal or non-lethal effects on prey (Van de Meutter et al., 2005). On the other hand planktonic organisms can detect the presence of potential predators through kairomons which enable them to reduce predation risk (Szulkin et al., 2006; Lass and Spaak, 2003; Beklioğlu and Jeppesen, 1999). Furthermore in response to fish kairomone zooplankton tend to reduce juvenile growth rate (Hanazato and Dodson, 1995), size at first reproduction (Von Bert and Stibor, 2006; Stibor, 1992), clutch size (Mikulski, 2001; Stibor and Lüning 1994), and body size (Brooks and Dodson, 1965). Not only life history adaptations but also morphological changes such as spin length, neckteeth provide zooplankton to avoid predation (Mirza and Pyle, 2009; Garza-Mouriño et al., 2005).

Thus prey actively defend themselves from predator with morphological (e.g. spins and helmet), physiological (e.g. toxins), life historical (e.g. delayed breeding) or behavior (predator avoidance behaviours) (Kavaliers and Choleris, 2001).

1.3. Avoidane Strategies of Zooplankton

Avoidance behaviour of zooplankton particularly the genus *Daphnia* has been well documented either vertical migration (Winder et al., 2003; Lampert, 2005; Lorke et al., 2008) or horizontal migration (Kvam and Kleiven, 1995; Lauridsen et. al., 1999; Burks et al., 2002). Diel Vertical Migration (DVM) which is based on the spending daylight hours in deep and at night move to the surface of lake has been studied almost for two centuries (Dodson, 1990). Also the reverse pattern has been seen (Armengol and Miracle, 2000).

This behaviour is one of the fascinating issues among limnologist since 1871 where Baron Cuvier confirms the existence of vertical migration among freshwater organisms (Carpenter and Kitchell, 1993). Although Baron Cuvier was known to observe this behaviour, August Weisman (1877) was the first researcher recorded diel vertical migration of zooplankton (Staker, 1974). After these finding, researchers has focused on the causes of behaviour. Some researchers such as Pennak (1944) and Welch (1952) thought that light is the most important factor in the existence of diurnal behaviour (Staker, 1974). The importance of light may be initiating, controlling and orientating the migration behaviour (Zaret and Suffern, 1976) because Bogorov (1946) and Buchanen and Haney (1980) found that there is no migration during the constant light of arctic summer in arctic waters (cited in Dodson, 1990). On the other hand Forel (1874) stated that blowing the wind direction may also affect the behaviour (Kikuchi, 1930). However many abiotic factors such as light, temperature may affect the diurnal movement as a cue; it is obvious that no single factor explain the behavioural variations (Carpenter and Kitchell, 1993). The field observations showed that there are four proximate factors (environmental cues or stimuli that appear migratory behaviour) which are light change, fish presence, food concentration and temperature triggers the DVM (Ringelberg and Van Gool, 2003).

However this well-known phenomenon is generally accepted as a result of compromise between food availability for feeding and predator avoidance for surveillance (Lorke at al., 2008) as avoiding visual predators, zooplankton leave warm, lighted and food-rich surface to cold, dark and relatively poor quality of food sources in deep layer (Lampert, 2005). In fact when the resource does not show any differences between upper and lower zone then the migration behaviour does not occur (Gliwicz, 1986).

Moreover availability of food controls the direction of vertical position (Beklioğlu et al., 2008). On the other hand ultimate causes or natural selection is involved such as Hairston's (1976) research on calanoid copepods that they do not migrate down during daytime in the fishless lake but stay at the surface for feeding (as cited in Dumont and Negrea, 2002).

This behaviour is definitely energetically advantageous in contrast to stay in cold, deep and poor food conditions but the most important factor is deeply pigmentation. The pigmented animals mostly found in mountain lakes, saline lakes and temporary pods. Pigment offer protection against radiation. Finally when the visual predator introduced pigmented animals are eliminated and unpigmented ones gain advantageous over pigmented ones (Dumont and Negrea, 2002). Although the migration pattern reduces the risk of predation it is costly (Winder et. al., 2003; Dodson, 1990) because the foraging ability of prey decreases while escaping from predators (Van Gool and Ringelberg, 2003). Also reduced food availability in the cold hypolimnion causes slower growth and lower fecundity (Lampert, 1989), so upward migration reflects the costs of staying in the low oxygen and food shortage (Loose and Dawidowicz, 1994). Previous researches are mostly express the vertical migration in deep lakes however recent researches showed that diel vertical migration occur not only in deep lakes but also in shallow lakes where the predation pressure is high (Meerhoff et al., 2007a; Iglesias et al., 2007). In shallow lakes although light may penetrate through the bottom of the lake and do not provide hypolimnetic refuge and depth gradient, zooplanktons develop alternative avoidance strategy (Nurminen and Horppila, 2002). Pelagic zooplankton may migrate into vegetated zone during day time which is termed as diel horizontal migration (DHM) (Burks et al., 2002).

The behaviour is known as 'shore avoidance' long ago by Hutchinson, (1969) that predation pressure in the littoral zone is higher than in the pelagic region (Semenchenko, 2008). The daytime aggregation under the lilies was first documented by Timms and Moss (1984) since then several researchers have examined the behaviour. Nevertheless small-sized species can also migrate horizontally under high predation pressure (Semenchenko, 2008; Lauridsen et al., 1996). For instance Hutchinson (1967) stated that the diurnal migration of rotifers less prominent than crustaceans but more extensive researches showed that rotifers also show this behaviour (George and Fernardo, 1970).

However, confronting with predators either in pelagic zone or littoral zone many prey avoids being predated so the avoidance must be balanced with the costs and benefits (Sagrario et al., 2009). As mentioned before submerged macrophyte and phytoplankton compete for resources thus there may be shift through clear to turbid conditions (Scheffer et al., 1993). Furthermore the competition between macrophyte and phytoplankton reduce food quality and quantity hence inhabiting within the macrophyte has an important cost (Burks et al., 2002). On the other hand, among macrophyte bed higher quantity of periphyton and bacteria serve as a life support system for zooplankton than open water (see in Burk et al., 2002). Finally the potential benefits of DHM are reducing being predated, consume alternate littoral resources whereas invertebrate predation may increase in littoral zone as well as consume poor quality of food are the main costs (Burks et. al., 2002). The refuge effect of macrophytes display differences between climatic regions but most of the DHM researches have conducted mainly in northern temperate lakes (Burks et al., 2002). In northern temperate lakes, submerged macrophytes influence the biodiversity and water transparency in shallow lakes (Declerk et al, 2005) whereas in subtropics and tropics the effects of macrophytes on trophic interactions are more complex than temperate regions. Abundant plant life forms create high predation pressure on zooplankton (Iglesias et al., 2007) due to existence of numerous small and juvenile fish into the vegetation (Meerhoff et al., 2007; Texiera de Mello et al., 2009). Hence the DHM is not very beneficial for zooplankton (Meerhoff et al., 2006) where the littoral planktivorous fish are abundant.

Furthermore, in the Mediterranean shallow lakes zooplankton may show similar predation risk in littoral macrophyte as determined in subtropical lakes (Castro et al., 2007).

1.4. Possible Refuges in Shallow Lakes

The refuge issue is very important due to its stabilizing force on prey-predator population dynamics (Berrymann and Bradford, 2006).

1.4.1. Submerged Macrophyte

Submerged macrophytes have critical role in freshwaters (Jeppesen et al., 1997) as well as their conservation and economic values (Timms and Moss, 1984). Submerged macrophytes have several stabilizing effects on water clarity as mentioned before however the most important role of stabilizing effects of submerged macrophytes on water clearance in euthrophic freshwater lakes is providing daytime refuge for cladocerans (Lauridsen et al.,1996, Scheffer, 1999). Furthermore presence of piscivorous fish creates predation pressure on planktivorous thus submerged plant provide spawning habitat and refuge for them as well as zooplankton (Persson and Eklöv, 1995; Genkai-Kato, 2007). Zooplankton generally aggregate inside or around the edges of macrophyte beds instead of outside (Cazzanelli et al., 2008). The refuge effects of macrophytes for zooplankton depends on the predacious macroinvertebrate assemblage within the plant hence this create risky habitats for zooplankton (Sagrario et al., 2009). Therefore dense macrophyte provides poor refuge because of macroinvertebrate density that increases with macrophyte density (Burks et al., 2001; Cattaneo, et.al, 1998). Thus besides predator, size, shape, plant architecture and density of plant patches affect the macrophytes refuge capacity (Jeppesen et al., 1997). For instance the high macrophyte edge: area ratio would prefer by migrating cladocerans while low macrophyte edge:area would prefer by non-migrating ones (Lauridsen et al., 1996).

As a well-known phenomenon that submerged macrophytes provide a refuge for zooplankton against predation but less is known about the role of emergent and floating-leaved plants. In turbid lakes, emergent and floating-leaved plants are dominant so these functional types of vegetation play an important role in the zooplankton migration via predator-free space (Cazzanelli et al., 2008). However submerged macrophytes have better refuge effect in temperate lakes than free-floatings (Meerhoff et al., 2003). In northern temperate lake, the refuge effect of submerged macrophyte is poor in oligotrophic conditions (Jeppesen et al., 1997), on the other hand the refuge effect of submerged macrophyte in mesotrophic and eutrophic conditions with submerged plant are relatively high (Jeppesen, 1997). Although the nutrient levels are low, macrophyte cover will decrease. According to climate changes researches indeed macrophyte dominance might be controlled by other factors instead of nutrient and depth especially in warm regions especially the fish composition may effect (Kosten et al., 2009). However submerged macrophyte and fish interactions are less studied in warmer climatic conditions (Meerhoff et al., 2003). In (sub) tropics numerous smallest fish aggregate within the macrophyte (Mazzeo et al., 2003) hence diminished the refuge capacity in subtropic lakes (Iglesias, 2007; Meerhoff et al., 2007b). For instance, in Andean Patagonian ponds emergent macrophyte (*Juncus pallescens*) may act as a refuge whereas the submerged macrophytes did not affect the horizontal movement (Trochine et al., 2009). Thus these conditions probably result strong predation pressure on zooplankton (Van Leewen et al., 2007). On the other hand water level fluctuations may affect submerged plant community for instance high water level may reduce light availability whereas low water level may damage plants through ice and wave during winter and desiccation during summer (Beklioğlu et. al., 2006).

1.4.2. Turbidity

According to EPA(1999), turbidity is defined as ‘‘principal physical characteristic of water and is an expression of the optical property that causes light to be scattered and absorbed by articles and molecules rather than transmitted in straight lines through a water sample’’. Suspended and dissolved matter such as clay, silt, organic matters (arise from erosion, decomposition of rocks, soil and dead plant material, plankton and other microscopic organisms) are causes of turbidity (Anderson, 2005; Bruton, 1985). In the regulation of water turbidity, sediment resuspension is the principal process (Horpilla and Nurminen, 2005). Also strong wind can create turbidity via mixing the water column (Scheffer, 1999) furthermore whereas seeking food by stirring the sediment, benthivorous fish could contribute turbidity (Parkos et al., 2003, Scheffer et al. 2003). Light has an important regulatory resource for the production of aquatic systems (Bramm et al., 2009).

For instance negative effects on light scattering of suspended particles provide refuge for zooplankton against visual predators (Horppila et al., 2004) especially in clay turbidity macrophyte have a poor refuge effect (Pekcan-Hekim, 2007). Furthermore competition between visual and tactile predators in low water clarity concluded the gain of tactile predator (Eiane et al., 1997; Nurminen et al., 2008a). Also planktivorous fish and phantom midge larvae may exist together in clay turbid lakes so these conditions create a negative impact on biomanipulation studies (Nurminen et al., 2008b). In clay-turbid lakes, turbidity is mainly caused by inorganic particles eroded from drainage areas or suspended from sediment (Niemistö et al.2005) and this affect the primary production by reducing the available light photons for phytoplankton and macrophytes (Lind 2003). However in high dissolved organic compound humic lakes where the light attenuation is strong (Kirk, 1994) reduce the reactive distance and predation rate of planktivorous fish. Moreover, the submerged vegetation is usually sparse instead of dense floating-leaved and emergent macrophytes species in humic waters (Estlander et al., 2009).

Thus these type of vegetation also be an important refuge for zooplankton against fish predation (Timms and Moss, 1984).

However in the absence of temperature and food gradients but predation pressure, the amplitude of vertical migration is mostly depending on the water transparency (Dodson et al., 1996; Alajarvi and Horppila, 2004; Semyalo et al., 2009), thus affect the reactive distance in the detection of prey (Nurminen et al., 2008b). Furthermore algae-induced turbidity may prevent foraging (Pekcan-Hekim, 2007), predator avoidance (Lehtiniemi et al., 2005) and refuge use of fish (Engsrom, et al., 2006). For instance, although pike larvae can detect predator by chemically and visually long-term turbidity may be critical for their survival (Lehtiniemi et al., 2005). Thus in the presence of non-toxic cyanobacteria decreases the feeding of pike larvae on zooplankton prey due to low vision (Engström-Öst et al., 2006). According to experiments using artificial plant beds showed that no clear aggregations occur in turbid lakes. This may reflect the reduced seeking plant refuge because of the availability of turbidity refuge (Schou et al., 2009).

1.4.3. Sediment

In benthic environments, activity and habitat choice of invertebrates are strongly affected by spatial heterogeneity and habitat complexity, making it likely those sediment characteristics can also influence predator–prey interactions (Gilinsky, 1984). Protection from predators in which choosing particular sediment, availability of food and protection from stressful physical conditions as ultimate factors however benefit cannot be achieve in every substrate type (Baumgartner et. al., 2003). On the other hand few species use the open water for breeding, feeding, growing and die however most use the bottom and edge habitats except deoxygenetion due to confine animal growth and survival (Moss, 1998).

In fact preference of submerged plant is the reason of avoidance mechanism against predator however existence of chemical cue induced the zooplankton seeking refuge to avoid predation. A laboratory experiment demonstrated that presence of cue trigger the cladoceran towards the sediment (Beklioğlu & Jeppesen, 1999).

1.5. General Characteristics of Zooplankton Groups

1.5.1. Cladocera

Morphological and taxonomical studies of cladocerans have begun in the second half of the 17th century. Although the figures of the cladocerans were schematic or allegoric, Goedardo (1662) and Swammerdam (1669) were the first researcher who isolated species of the genera *Daphnia* O.F. Müller, *Polyhemus* (L.) and possibly *Simocephalus* Schoedler, *Scapholeberis* Schoedler and *Moina* Baird. However Schaeffer (1763) pointed out the detailed description of *Daphnia magna* Straus. In 1776, Otto Friedrich Müller divided Cladocera into three genera: *Daphnia, Lynceus* and *Polyhemus*. This work was the pioneer one for researchers whom mentioned species of Cladocera described by O.F. Müller and used his figures during the following 30 years. Finally the Cladocera were recognized as an independent group by the end of the 1820s (cited in Korovchinsky, 1997).

Cladocerans (Crustacea: Anomopoda) are very important role in the aquatic food web due to energy transfer from primary producers to consumers (Sarma et al., 2005; Dodson and Frey, 2001; De Bernardi et al., 1987).

According to Forro et. al., (2008), recognised four cladoceran ordo: Anomopoda, Ctenopoda, Onychopoda, and the monotypic Haplopoda**.** Most of the Cladocera species are filter-feeders that feed on phytoplankton, bacteria and detritus while onychopods and haplopods are predatory.

In the littoral zone of lakes, there can be high diversity of cladoceran (Forro et al., 2008) and these species are mainly feed on water-substrate interface by scraping algae and detritus from surface or from sediments consists of phytoplankton, bacteria, protozon, periphyton and detritus (Kuczynska-Kippen, 2009; Balcer et al., 1984). General characteristics of Cladocera are the large compound eye and five pairs of lobed, leaf like thoracic legs (Fig. 1.1). Although the true abdomen suppressed, at the end of the body there is a postabdomen.

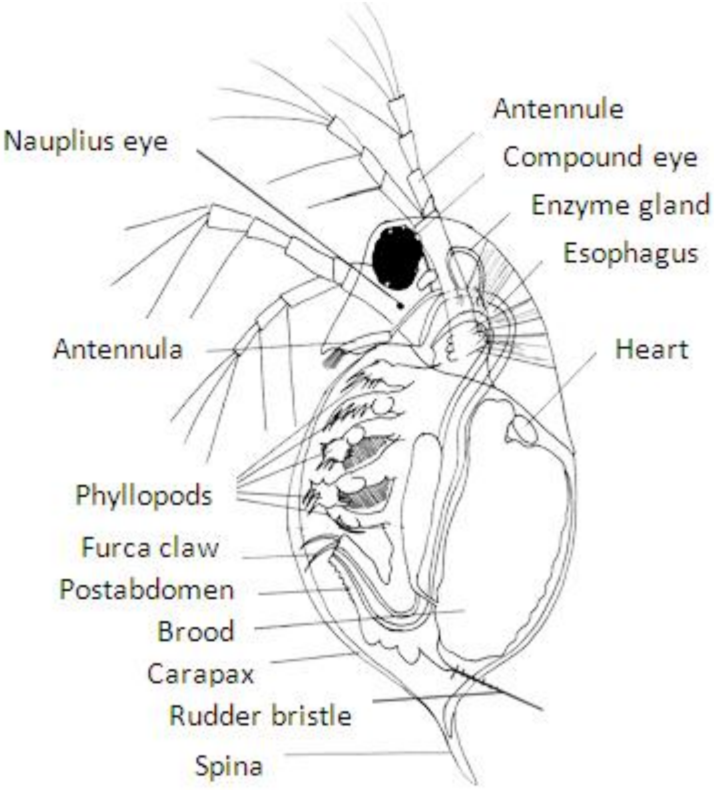


Figure 1.1. Anatomy general characters of cladocera.

(Taken from http://www.cladocera.de).

1.5.2. Copepoda

Copepods, known as ‘oarsmen’, have segmented cylindrical bodies. The head segments of copepods are fused and covered by carapace (Fig.1.2). The first antenule consists of 8-25 segments which are used for locomation and chemo/mechanoreception (Balcer et al., 1984). Copepods are mainly common and diverse in marine systems than freshwater. Copepoda are represented by three different groups: Calanoida which is primarily filter-feeder throughout their whole lifespan and Cyclopoida which is mostly predaceous in their adult phase with their modified mouthparts (Gliwicz, 2004). These reptorial cyclopoids may be herbivores, omnivores or carnivores as for harpacticoids which are bentic organisms feed on detritus (Pennak, 1989).

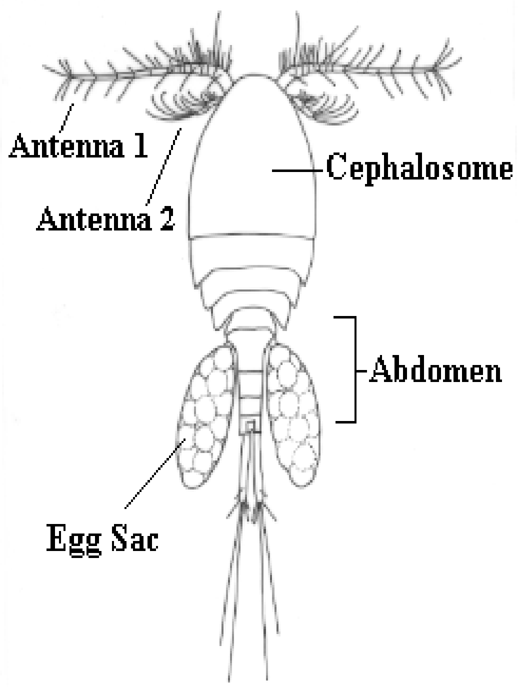


Figure 1.2. Anatomy general characters of cladocera.

(Taken from http://museumvictoria.com.au.)

1.5.3. Rotifera

Rotifers were first studied and described by Leeuwenhoek in 1703 since then rotifers have great concern by most of the researchers (Pennak, 1989). Rotifers are the primary freshwater metazoan. The major groups of this phylum are Monogonanta and Bdelloidea (Segers, 2008). Body of rotifera consists of head which is not distinct from the body. Most characteristics morphology of rotifera is their transparency which enables to observe internal organs. At the top of the head there is a ciliary organ called ‘corona’ that used for swimming and food intake. Rotifers can feed on small algea, detrital particules or bacteria. Rotifers have several sense organs including sensory bristles and finger like palp (Fig. 1.3). Morphologically the body of rotifers may be cylindirical, sack- or belly-shaped or laterally or dorsoventrally flattened. Flexibility of rotifers depends on the cuticle or skin. In many species cuticle forms a shell called ‘lorica’. Lorica is an important diagnostic character as well as presence/absence of foot. In loricate rotifers foot is retractile through lorica on the other hand in non-loricate rotifers, foot drawn up into the body (Pontin, 1978). Rotifers can be found almost all type of freshwater habitats and mostly diverse in littoral zone of stagnant waterbodies (Segers, 2008). Although cladocerans and copepods are the dominant organisms rotifers supply largely to the biomass and productivity of zooplankton community. Thus there is a strong predation pressure on rotifers by most of the invertebrate predators (Williamson and Butler, 1986).

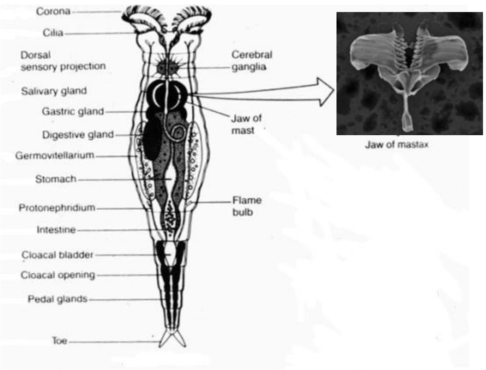


Figure 1.3. Morphology of general characters of Rotifera.(source:SEM of the mastax http://scrubmuncher.wordpress.com/2012/02/13; figure taken from http://educationally.narod.ru/freshwaterlife1photoalbum.html)

1.6. Size Structure of zooplankton

Size of the zooplankton groups shows broad range. For instance the size of “water fleas” is varying in between 0.2-3mm, and for *Leptodora kindtii* which is the largest cladoceran can reach up to 18mm (Forrỏ et. al., 2008). Furthermore, the body size of copepods is ranging between 0.3-3.2mm long (Forrỏ et. al., 2008). Rotifers are the smallest group among others ranging between 0.1-0.5mm in size (Pennak, 1989). Zooplankton groups can be found almost in all type of water bodies and inhabited different zone of lakes and can consider open water (pelagic) or plant associated/benthic species (Fig. 1.4).

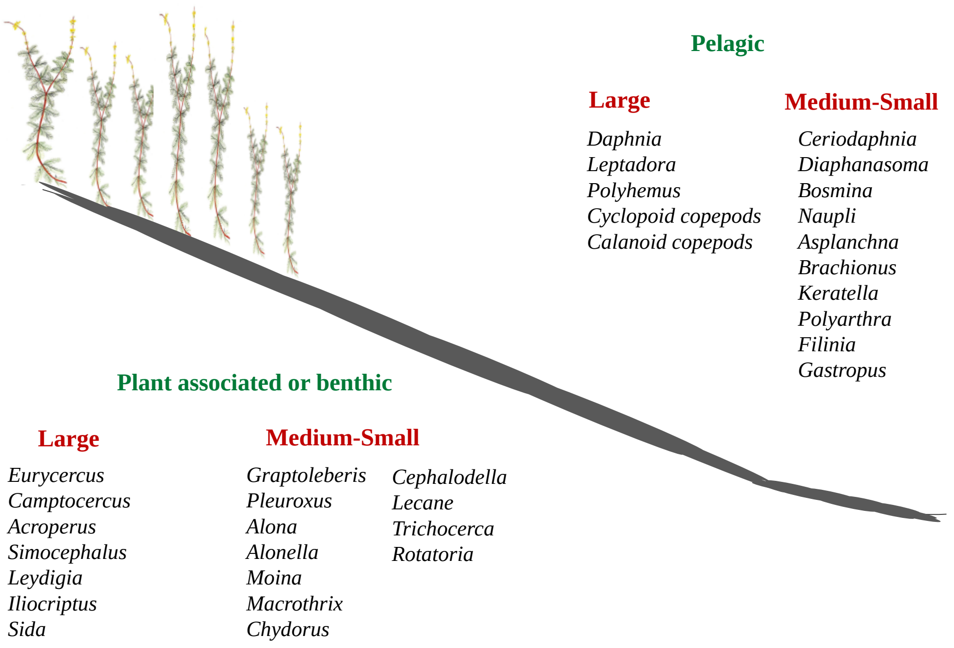


Figure 1.4. Habitat choice of zooplankton size groups.(Modified from O'Sullivan, 2004 and Gyllström et al., 2005).

Body size is an indicator of predation pressure (Brucet et al., 2010). According to Gillooly & Dodson (2000), cladoceran mean body size has become smaller towards lower latitudes.

However Gyllström et al., (2005) suggested that cladoceran body size did not show any trend along European latitudinal gradient despite lack of large bodied *Daphnia* spp. exist in the warmer lakes. Accordingly, large sized *Daphnia* was also observed in sub(tropic) shallow lakes (Meerhoff et al., 2007a; Lancelot, 2010).

Furthermore, brackish lakes in Mediterranean region were mostly dominated by rotifers while in cold Danish lakes consisted of both cladocerans and copepods (Brucet et al., 2010).

The occurrence of smaller taxa and individuals in warm lakes is as a consequence of dense predation pressure (Meerhoff et al., 2007a; Brucet et al., 2010; Iglesias et al., 2011).

1.7. Zooplankton Researches in Turkey

According to a recent check-list for zooplankton research in Turkey (Ustaoğlu, 2004), the researches has begun at the beginning of 20th century by Daday (1903), Vavra (1905) and Zederbauer & Brehm (1907). After these years there is a big gap in zooplankton researches in Turkey until 1950s with the exception of two papers by Mann (1940) and Geldiay (1949). In the following years, however, fauna of Cladocera, Copepoda and Rotifera were investigated intensely by foreign researchers (as cited in Ustaoğlu [2004a]: Muckle, 1951; Kiefer, 1952, 1955; Lindeberg, 1953, 1955; Noodt, 1954; Hauer, 1957; Margaritora and Cottarelli, 1970). After 1970s Turkish scientist’s investigations have increased (ca. 120 published papers). Since then many new species were identified (e.g. Gündüz, 1990 and 1996) and recorded from inland waters (e.g. Akbulut (Emir), 2001; Ustaoğlu et al., 2004a,b; Aygen & Balık, 2005; Akbulut (Emir) and Kaya, 2007; Sönmez et al., 2008; Bekleyen et al., 2011; Erdoğan & Güher, 2012, Ustaoğlu et al., 2012a). However most of these valuable papers are taxonomic researches based on the inventory of inlands and there are few studies on zooplankton and predator interaction as well as zooplankton effects on water quality.

1.7. Objectives

The main aim of this thesis is to determine the factors which may have combined impact with ongoing warming influencing zooplankton community structure in Turkish Shallow Lakes as an implication of Mediterranean region. Furthermore, to investigate the habitat preference of zooplankton under the predation pressure in shallow lakes.

- ✓ Which factors influencing zooplankton size structure along the latitudinal gradient in Turkey? (Chapter 2)
- ✓ How zooplankton size structure and their diel movements are changing in different habitats (plant and open) for Mediterranean shallow lakes? (Chapter 3)

- ✓ Do submerged plants provide refuge for zooplankton under the predation pressure as observed from north temperate shallow lakes? (Chapter 4)

- ✓ According to the long term data set which covers 15 years how was the zooplankton community composition change and which was the main driving force on this change throughout the years? (Chapter 5)

To address these questions, four different approaches were used in this thesis because no single approach can explain the questions. Controlled experiments were performed both in laboratory and *in-situ* mesocosm experiments. Following snap-shot sampling 31 lakes were sampled from 41º 49' N to 36º 41' N, to evaluate the latitudinal differences. Finally, to understand the relations through time scale, long term monitoring data were used in two shallow lakes located in central Anatolia.

CHAPTER 2

TOP-DOWN VERSUS BOTTOM-UP FACTORS THAT CONTROL THE COMMUNITY STRUCTURE OF ZOOPLANKTON IN 31 ANATOLIAN SHALLOW LAKE

2.1. Introduction

In Turkey, according to the Kazancı et al. (1995) there were approximately 200 natural lakes which are mostly consisted of shallow, 75 dams and 700 ponds however, many of them lately dried out due to surface and groundwater abstraction for irrigation (e.g. Akşehir, Bolluk, Tersakan, Yarışlı, Yazır etc., wwf, 2010; Durduran, 2010) and 218 dams were constructed since 1995 (DSİ, 2012) (Fig. 2.1.).

Figure 2.1. Some of the dried lakes in Turkey. (Taken by METU, Limnology Lab, 204).

Furthermore, in Turkey freshwaters were mostly valued for human use purposes such as irrigation for agriculture, electricity production, domestic use and discharge of domestic wastes (Beklioğlu et al., 2001) thus lakes were subjected to eutrophication (nutrient enrichment; P, N) as well as large water level fluctuations. The latter may also induce salinization depending on extend of water level drop which may set the lake water level below the outflow that may trigger salt accumulation through high evaporations in summer. In addition to these, there is a warming trend as a reflection of global climate change since 1990s in Turkey (Türkeş et al., 1995, 2002; Kadıoğlu, 1997; Tayanç et al., 1997, 2009; Şensoy et al., 2008). This may also further enhance evaporation.

Ongoing warming, nutrient enrichment and water abstractions have had negative effects on ecosystem structure and function that resulted in further eutrophication of lakes through reduced nutrient retention capacity (Özen et al., 2010). Further lakes in lower latitude reached to turbid state more rapidly than northern temperate lake for the same perturbation levels (Romo et al., 2004). In addition, high temperature and low water level conditions may worsen the ecosystem dynamics of Turkish shallow lakes.

Moreover, according to the cross comparisons, fish community composition has changed towards smaller, spawn earlier, grow faster as well as became omnivorous (Lappalainen & Tarkan, 2007; Meerhoff et al., 2007b; Blank & Lammouroux, 2007; Teixeira-de Mello et al., 2009; Jeppesen et al., 2010a) in warmer lakes compared to the high latitude northern lakes. Thus, fish can have a strong top-down control on large bodied zooplankton in turn to control on phytoplankton in low latitudes lakes (Moss et al., 2004; Meerhoff et al., 2007b). Furthermore, several studies indicated that the small fish aggregate submerged plant beds in warm lakes (Iglesias et al., 2007; Teixeira-de Mello et al., 2009; Jeppesen et al., 2010a; Gelos et al., 2010) thus eliminating the day time refuges effect for zooplankton against fish predation that is major predator avoidance strategy for shallow lakes (Lauridsen & Lodge, 1996; Burks et al., 2001).

Therewith, plant may not provide a daytime refuge to zooplankton consequently the migration pattern may change through dwell on the sediment during day time and during night where the visual hunting predators have difficulties ascend to the surface (Gliwicz, 1986; Dodson, 1990; Castro et al., 2007; Meerhoff et al., 2007a; Tavşanoğlu et al., 2012).

Furthermore, the risk salinization induced through drought or reduced water level can be a major problem for survival of zooplankter especially cladocera (Williams, 1987; Schuytema et al., 1997). The increased salinity has already reported in Anatolian basin (Beklioglu & Tan 2008; Beklioglu et al. 2011). Particularly during the dry period between 2003-2008, the salinity was increased a threefold in Lakes Eymir and Mogan where they located in the central Anatolia (Beklioglu et al. 2011). The negative impacts of salinity such as decreased fecundity, slower somatic growth and increased mortality were reported several papers for Daphnia (Hart et al. 1991; Hall and Burns 2002; Grzesiuk and Mikulski 2006; Sarma and Nandini 2006; Bezirci et al., 2012). Furthermore, with increasing salinity, the species richness and size diversity decreased excluding marine species (Boix et al., 2008; Brucet et al., 2009). In addition, fish community may change through small bodied and/or plankti-omnivorous species towards increased salinity, accordingly reinforced to the effects of eutrophication (Jeppesen et al., 2010a).

The knowledge on the limnological processes for arid to semi- arid Mediterranean shallow lakes are poor (Alvarez Cobelas et al., 2005). Likewise in Turkey, despite there are several valuables literatures on the zooplankton community of shallow lakes, most of them were concentrate on a single or a few lakes with high taxonomic studies (e.g. Gündüz, 1997; Altındağ & Yiğit, 2002; Güher & Kırgız, 2004; Ustaoğlu, 2004b; Akbulut & Kaya; 2007; Kaya & Altındağ, 2009; 2010; Kaya et al., 2010; Erdoğan & Güher, 2012).

The present study focused on the impacts of zooplankton community structure with a large spatial resolution (31 lakes) along a latitudinal gradient from 41°N to 37°N spanning over 5 latitudes. The major aims of this study were 1) to use size and taxon based approaches to investigate the differences in zooplankton community structure in study lakes 2) to elucidate the factors influencing zooplankton size structure along the latitudinal gradient in Turkey.

2.2. Material and Methods

2.2.1. Snap-shot sampling methodology

Based on space-for-time substitution approaches, lakes were sampled using snap shot sampling protocol along a latitudinal gradient from the north to the south of western Turkey. The further detail of snap-shot sampling protocol was described by Moss et al., (2003). There has been several international large consortium projects (European Unioun 5th and 6th frameworks funded, acronym: Ecoframe, Bioman and Eurolimpacs; South American Lake Gradient Analyses) (Gyllström et al., 2005; Jeppesen et al. 2010b; Kosten et al., 2009, 2011) was widely tested the protocol. Accordingly, the physical, chemical and biological variables in each lake were employed in each lake (Fig. 2.2.). This study has funded by TUBITAK 105Y332; TUBITAK 110 Y 125, METU-BAP (BAP-07-02-2010-00-01) and REFRESH (EU-FP7-20091). The physical, chemical and biological data excluding zooplankton were taken from Beklioğlu et al.,(in prep.). Thus the data excluding zooplankton will have used in the PhD thesis who have carried out their thesis at METU, Limnology Laboratory (Ayşe İdil Çakıroğlu, Eti Ester Levi, Gizem Bezirci, Şeyda Erdoğan) as well as completed PhD thesis (Arda Özen).

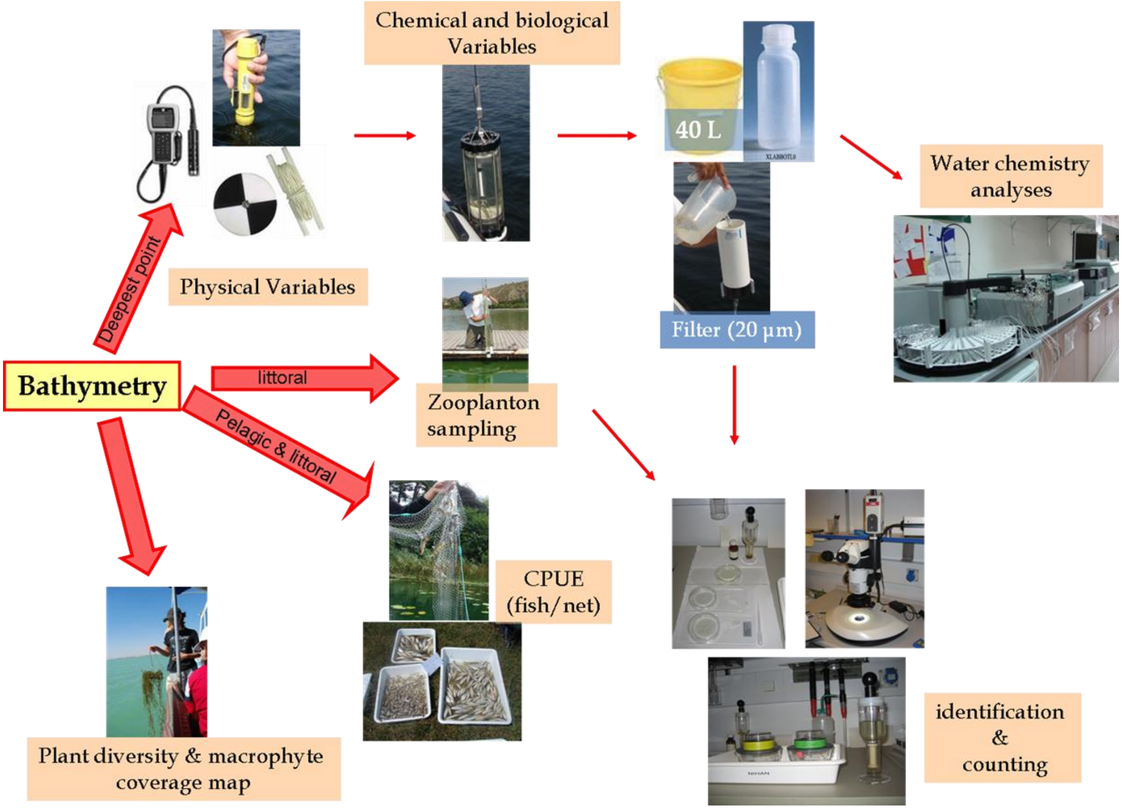


Figure. 2.2. Schematic diagram of lake snap-shot sampling methodology

Before determining the general physical and chemical characteristics of the study lakes, bathimetry was carried out to determine the deepest point of the lakes. Deph measurements were performed by using Depthmate Portable Sounder (Speectech *SM*-5) along the parallel and vertical transect lines depending on lake size. Due the protocol all the physical and chemical parameters were taken from the deepest point of the lakes therefore batimetry was the first step of the sampling campaign. From the deepest point, conductivity (±1 μS cm-1), pH(±0.2), salinity (±2 mg chloride L^{-1}), temperature (◦C), dissolved oxygen (mg L^{-1}) were measured by using a YSI 556 multiprobe. Contemporarily water samples for chemical analysis (total phosphorus (TP), total nitrogen (TN), soluble reactive phosphate (SRP), alkalinity and chlorophyll *a* (Chl *a*) and biological variables (zooplankton) were taken from depth-integrated, mixed samples (40L) from the entire water column at mid-lake stations located in the pelagic (deepest part) with using a KC Denmark Water Sampler (3.5 L). Samples for chemical analysis were kept frozen until analyses. Furthermore, 20L of water (within 40L mixed sample) were also filtered with a 20 μm mesh size filter for zooplankton. Whereas in the littoral part of the lake, zooplankton samples (20L) were taken with using 1m Plexi Glass Tube Sampler and filter all water with a 20 μm mesh size filter and fix within 4% lugol solution.

We performed fishing with Lundgrens multi-mesh gill nets (length 30 m; height 1.5 m; 12 panels with mesh sizes (knot to knot) of 5.0, 6.25, 8.0, 10.0, 12.5, 15.5, 19.5, 24.0, 29.0, 35.0, 43.0 and 55.0 mm) depending on lake size. The nets were set overnight both parallel to the littoral and open water zone of the lake for an average duration of 12 hours. Fish were identified, counted, measured (total length) and weighed (fresh mass).

Aquatic macrophytes (floating-leaved and submerged) were investigated in each lake. Percent plant covers of lakes were estimated via floating-leaved and submerged macrophyte data along the parallel transect lines depending on lake size.

On the other hand, percent plant volume inhabited (PVI %) was calculated from:

%PVI= (%c * p) /wd

where:

c: plant coverage; p:average plant height and wd: water depth

All zooplankton taxa were identified to genus or species level whenever possible and counted 50-100 individuals of the most abundant taxa. Countings were performed at the magnification of X40 (Cladocera and Copepoda) in a stereomicroscope (LEICA MZ 16) and X60 (rotifers) in an inverted microscope (LEICA DMI 4000). For taxonomical identification, the keys developed by Scourfield ve Harding (1966), Ruttner-Kolosko (1974), Koste (1978), Pontin (1978), Einsle (1993), Segers (1995), Smirnov (1996), Flö*β*ner (2000), Smith (2001) were used. We classified *Daphnia*, and *Simocephalus* as large bodied and, *Bosmina*, *Chydorus*, *Alona*, *Pleuroxus*, *Moina* *Ceriodaphnia* and *Diaphanasoma* as small-medium bodied cladocerans. We measured body size of around 25 individuals of each taxon whenever possible and calculated body weight from length using published relationships from the literature (Dumont et al., 1975; Bottrell et al., 1976; McCauley, 1984). We converted the biovolume of rotifers to dry weight according to Dumont (1975); Ruttner-Kolinsko (1977) and Malley et al., (1989).

Samples for chemical analysis were frozen until analyses. For total phosphorus (TP), the acid hydrolysis method was used (Mackereth, Heron & Talling, 1978). For total nitrogen (TN) analysis Scalar Autoanalyzer Method was used (San++ Automated Wet Chemistry Analyzer, Skalar Analytical, B.V., Breda, Netherlands). The chlorophyll *a* was determined using ethanol extraction (Jespersen & Christoffersen, 1987) and the absorbance measured at 663 and 750 nm.

2.2.2. Study sites

Environmental and biological variables were taken during the peak of growing season (August-September) of 2006, 2007, 2008, 2009 and 2010. During the sampling period, 31 lakes were sampled (Fig. 2.3., Table 2.1.; Appendix A) along the latitudinal gradient from Kırklareli (41° 49′ N; 27º 57′ E) to Muğla (36° 41′ N; 28º 50′ E). Furthermore, the location of sampled lakes was represented by different climatic conditions such as large steppe climate to maritime temperate, however, most part of the country prevail Mediterranean climates (Şekercioğlu et al., 2011) (Fig. 2.4.).

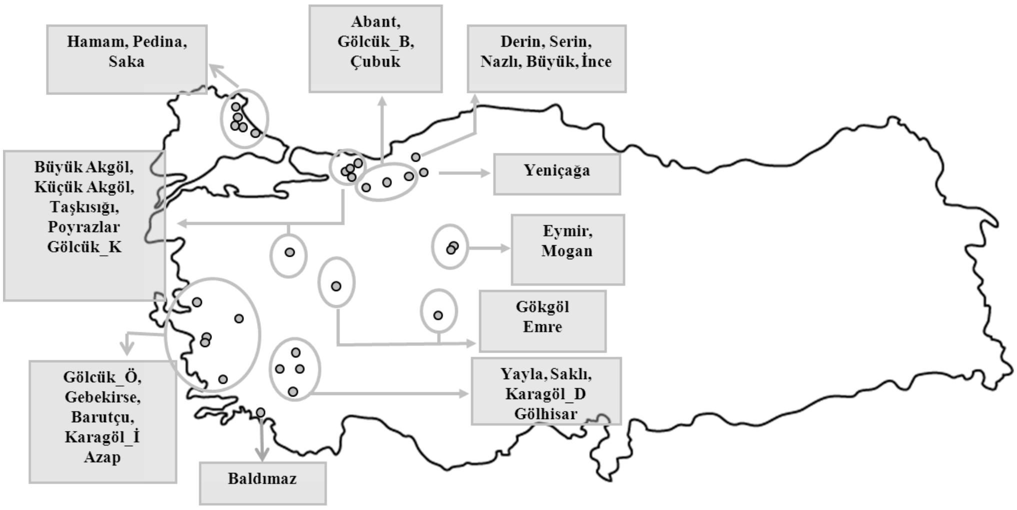


Figure. 2.3. The location of study sites.

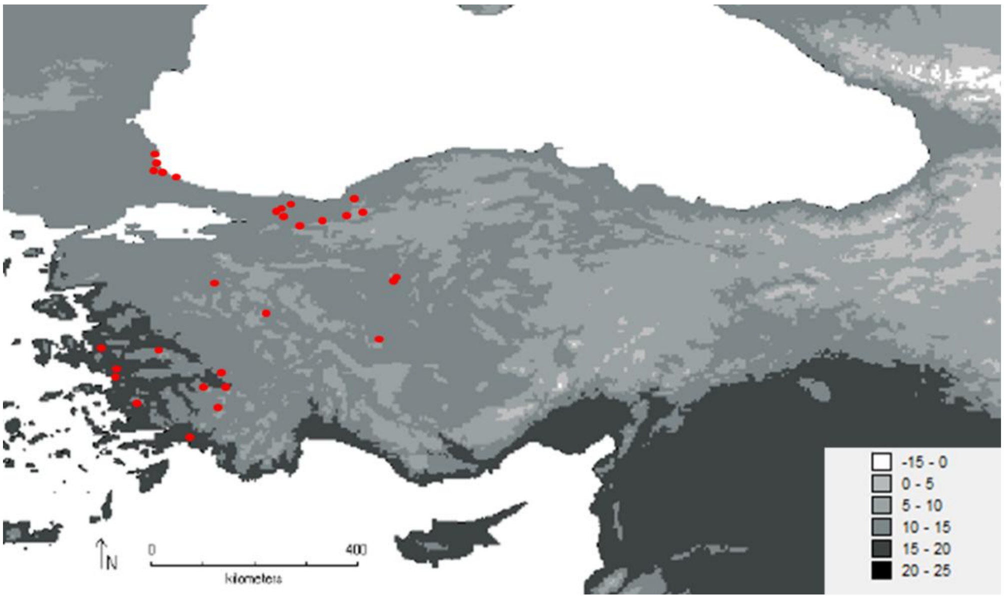


Figure 2.4. Selected sampling sites located different climatic conditions along Turkey. Grey scale gradient (grey to white) represent the decrease mean temperature from 15-20 to <0 ºC. Data source: www.wordclim.org.

Table 2.1. Physical, chemical and biological characteristics of the study lakes given as the range, mean and median of each variable. (n=31).

Variables	**Range**	**Mean**	**Median**
Altitute (m)	1-1328	657	813
Lake size (ha)	0.10-635	91	25
Maximum Depth (cm)	55-1740	427	340
Surface Water Temperature (°C)	18-32	24	25
Salinity (‰)	0.06-4.76	0.66	0.15
Conductivity ($\mu S\ cm^{-1}$)	130-8582	1248	303
Dissolved Oxygen ($mg\ L^{-1}$)	0.58-15.32	6.60	7.52
pH	6.92-9.64	8.31	8.19
Suspended Solids ($mg\ L^{-1}$)	4-75	31	22.60
Secchi Depth/Maximum Depth	0.05-1.00	0.32	0.26
Total Phosphorus ($\mu g\ L^{-1}$)	15-633	128	76.87
Soluble Reactive Phosphate ($\mu g\ L^{-1}$)	5-188	39	18.24
Total Nitrogen ($\mu g\ L^{-1}$)	239-2180	1081	954.74
NH_4 ($\mu g\ L^{-1}$)	3-565	141	68.78
NO_2+NO_3 ($\mu g\ L^{-1}$)	2-157	34	21.40
Alkalinity ($meq\ L^{-1}$)	0.50-11	3	1.5
Chlorophyll *a* ($\mu g\ L^{-1}$)	2.4-95	20	10.97
Plant Volume Inhabited (%)	0.00-69	12	3.64
Piscivorous fish (number of fish $net^{-1}\ night^{-1}$)	0.00-46	10	0
Plankti-omnivorous fish (number of fish $net^{-1}\ night^{-1}$)	0.00-1159	149	76

2.2.3. Statistical Analysis

To test the correlations between different environmental variables, Pearson correlation analysis (significance level $\sigma = 0.05$) was carried out (Table 2.2.). Prior to the analysis, the variables were transformed ($\log_{10}$, $\log_{10}+1$, or squared root) if the requirement of the normality not met which was tested by using Kolmogorov-Simirnov test in SigmaStat 3.5 (Systat software Inc.). All the mean data were given with ±1 standard error.

The multiple regression analyses (stepwise procedure, variables entered the analyses if $p \leq 0.1$) were performed to identify the relationship between zooplankton community parameters and possible effect of the independent variables which included TP, latitude, PVI% and mean density of fish per lakes. In each multiple regression, data were investigated in three ways: *i*) To examine the responses of zooplankton biomass and community composition; *ii*) To evaluate the size structure of zooplankton into the different habitat (open-littoral); *iii*) To assess the possible effects of trophic structure (top-down and bottom-up forces).

The Piecewise regression which was useful technique for estimating ecological thresholds was used to identify sharp increase/decrease of zooplankton based on the TP levels. The analyses were performed in SigmaStat 3.5. Furthermore, one-way analysis of variance (one-way ANOVA) was used for statistical comparisons.

To test the hypothesis size based approaches were used particularly for size diversity estimation. In the calculation of size diversity for zooplankton, the procedure given by Quintana et al. (2008) was followed. The proposed size diversity (μ) is computed based on the Shannon diversity index adapted for a continuous variable, such as body size. This measure takes the form of an integral involving the probability density function of the size of the individuals described by the following equation: where $p_x(x)$ is the probability density function of size x.

Nonparametric kernel estimation was used as probability density function after data standardization using division of sample data by their geometric mean value. We calculated the average size diversity of zooplankton in each lake was calculated.

Table 2.2. Results of Pearson correlation for the environmental variables in 31 lakes. Eva-Prec: Evapotransporation-Precipitation; Temp: Temperature; Alt: Altitude; Lat: Latitude; Sec/MxD: Secchi depth/Max depth; Chl *a*: Chlorophyll *a*; SS: Suspended Solids; TN: Total Nitrogen; TP: Total Phosphorus; SRP: Soluble Reactive Phosphorus; Cond: Conductivity; Sal: Salinity; Fgr: Biomass of Fish; Fcpue: catch per unit effort of fish; PVI: Plant Volume Inhabitat.

	Eva-Prec	**Temp**	**Alti**	**Lat**	**Sec/MxD**	**PVI**	**Chl *a***	**SS**	**TN**	**TP**	**SRP**	**Sal**	**Cond**	**Fgr**	**Fcpue**
Eva-Prec	1.00	0.33	0.03	**-0.79**	-0.08	-0.02	**0.39**	0.06	**0.49**	0.22	**0.36**	**0.49**	**0.59**	-0.14	-0.22
Temp		1.00	**-0.38**	**-0.51**	**-0.36**	-0.13	**0.42**	**0.47**	**0.66**	**0.38**	**0.45**	**0.50**	**0.53**	-0.33	0.26
Alti			1.00	-0.06	0.01	0.06	-0.13	-0.18	-0.10	-0.04	0.08	-0.31	-0.27	0.10	**-0.50**
Lat				1.00	0.17	0.24	-0.34	-0.14	**-0.46**	-0.15	**-0.36**	**-0.55**	**-0.60**	0.15	0.16
Sec.Dep					1.00	**0.38**	**-0.45**	-0.33	**-0.43**	**-0.50**	**-0.53**	-0.13	-0.11	0.12	-0.12
PVI						1.00	-0.19	0.01	-0.11	-0.08	**-0.36**	-0.23	-0.24	0.16	0.16
Chl *a*							1.00	**0.37**	**0.68**	**0.68**	**0.56**	0.11	0.19	0.13	**0.36**
SS								1.00	0.26	**0.39**	0.23	0.04	0.09	0.08	0.34
TN									1.00	**0.69**	**0.73**	0.30	**0.38**	-0.09	0.31
TP										1.00	**0.83**	0.14	0.21	0.12	**0.41**
SRP											1.00	0.35	**0.46**	-0.09	0.13
Sal												1.00	**0.95**	**-0.43**	-0.22
Cond													1.00	**-0.40**	-0.19
Fgr														1.00	**0.46**
Fcpue															1.00

2.3. Results

Due to the Anatolian plateau being relatively high elevation (average elevation 1100 m.a.s.l.), the altitude of the selected 31 lakes were ranging from 1 to 1328 m. Furthermore, surface area of the lakes was ranging from 0.10 to 635 ha (Table 2.1.). Moreover, the nutrient concentrations of the lakes were varied (ranging from 15 to 633 μg L^{-1} and 239-2180 μg L^{-1}, for TP and TN respectively). Secchi depth: Max depth and Chl *a* concentration had a wide range from 0.05 to 1 and 2 to 95 μg L^{-1}, respectively (Table 2.1.). Salinity and conductivity also displayed high variety among lakes (0.06-4.76‰ and 130-8582 μS cm^{-1}). Among 31 lakes, 10 of the lakes had no submerged plants and the maximum PVI % of the lakes was 69 (Table 2.1.). The CPUE net^{-1} $night^{-1}$of fish mostly composed of plankti-omnivorous fish (mean 149±3.5) while the CPUE net^{-1} $night^{-1}$ of piscivorous fish was very low (mean 6±0.8).

The results of multiple regressions were given as zooplankton community variables including all taxa as well as key species *Daphnia*, size and habitat was isvestigated by using two functional taxanomic group which was “small” and “large”, and trophic structure that top-down and bottom-up forces (Table 2.3.). The three steps of multiple regression were explained in detail at the below section.

Table 2.3. Results from the stepwise multiple regressions for 31 lakes. All variables were transformed. Biomass data were used for the zooplankton variables. Fish is expressed as individual net^{-1} night^{-1}. Zooplankton variables are given as µg L^{-1}. Zoop: zooplankton biomass; Tot. Zoop: total zooplankton; Cln. Cop: Calanoid copepods; Cyc. Cop: Cyclopoid copepods; SD: size diversity; MBS: mean body size; LPel: Large pelagic; LLit: Large littoral; SPel: Small pelagic; SLit: Small littoral; Chl a: chlorophyll a; TP: total phosphorus; TN: total nitrogen; Pla: planktiomnivore fish; Phyto: phytoplankton. Probability level of partial correlation coefficients are denoted as: <0.1†, <0.05*; <0.01**, <0.001***.

	Partial Coefficients				Regression statistics		
Variables	TP	Latitude	PVI	Fish		r^2	p
		Zooplankton community variables					
Tot. Zoop	0.52*				$F_{1,29}$=10.67	<0.05	0.27
Cladocerans	0.58**				$F_{1,29}$=14.3	<0.001	0.33
Daphnia	0.47**			-0.39*	$F_{2,28}$=3.07	<0.5	0.25
Copepods	0.39*				$F_{1,29}$=5.06	<0.05	0.15
Cln. Cop						ns	
Cyc. Cop	0.41*				$F_{1,29}$=5.61	<0.05	0.16
Rotifera						ns	
Naupli						ns	
ZoopRichness			0.40*		$F_{1,29}$=5.66	<0.05	0.16
		Size and Habitat					
Zoop SD						ns	
Zoop MBS		0.32†			$F_{1,29}$=1.88	<0.1	0.11
LitZoopSD		0.41*		-0.39*	$F_{2,28}$=4.77	<0.02	0.25
PelZoopSD						ns	
LPelZoop	0.36*				$F_{1,29}$=4.49	<0.05	0.13
SPelZoop		-0.68†		0.68***	$F_{2,28}$=9.15	<0.0001	0.50
LLitZoop	0.42*				$F_{1,29}$=2.34	<0.1	0.20
SLitZoop		-0.48**		0.67***	$F_{2,28}$=13.9	<0.0001	0.49
		Trophic Structure					
Chl a	0.68***				$F_{1,29}$=25.3	<0.001	0.47
Chl a:TP	-0.37*	-0.37*			$F_{2,28}$=3.78	<0.05	0.21
TN:TP	-0.73***	-0.57***			$F_{2,28}$=20.2	<0.0001	0.59
Pla :Zoop	-0.41*	-0.41*			$F_{2,28}$=4.74	<0.05	0.25
Zoop:Phyto	0.32†				$F_{1,29}$=1.96	<0.1	0.12
Salinity		-0.54***			F1,29=12.4	<0.001	0.29
<10cm:totFsh				0.59***	$F_{1,29}$=15.7	<0.001	0.35
Fish MBS		0.47**		-0.76***	$F_{2,28}$=21.1	<0.0001	0.60

2.3.1. Zooplankton community assemblage

The zooplankton of the studied lakes involved 31 cladoceran, 48 rotifers and copepods (both calanoid and cyclopoid) species (Appendix B). Cladoceran species mostly belong to the family Chydoridae while the most representative family among rotifers was Brachionidae.

According to the multiple regression analyses, TP was the most important predictor among other variables (Table 2.3.) in the explanation of the zooplankton community structure. Total zooplankton biomass including cladocerans and copepods were positively related to TP. Furthermore, the biomass of *Daphnia* and cyclopoid copepods were both increased with the increasing TP. However rotifers and naupli were not display significant relation with the other explanatory variables. According to the piecewise regression results, 110µg L^{-1} ($r^2=0.21$, $p<0.1$) of TP was observed as a change point for the total zooplankton and the biomass of total zooplankton increased significantly with the increasing TP (one way ANOVA, $F_{1,29}=7.15$; $p<0.05$) (Fig 2.5.).

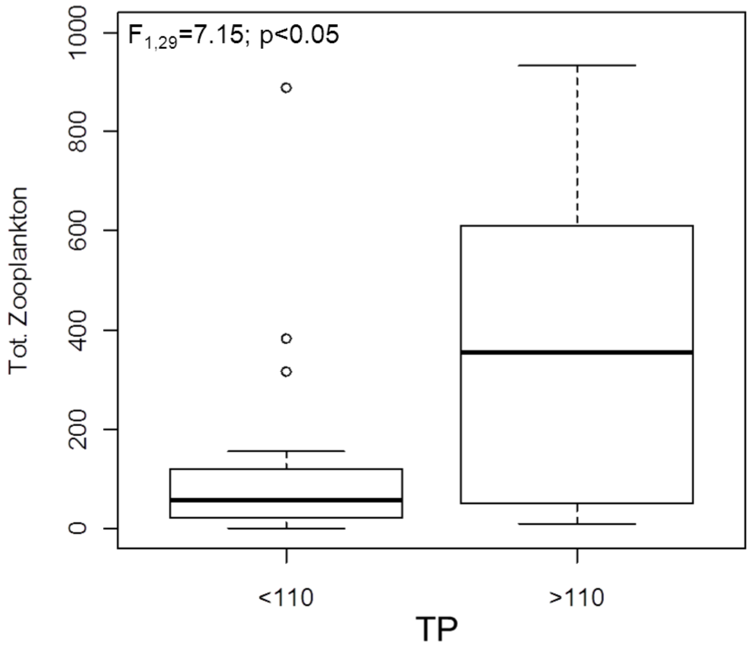


Figure 2.5. The relationship between total phosphorus (TP) and the biomass of total zooplankton (μg L^{-1}). Box plots show the 25%, 50% and 75% percentiles for two total phosphorus levels.

The zooplankton community composition also displayed remarkable differences between threshold TP levels (Fig. 2.6.). Particularly small sized groups (*Bosmina*, *Chydorus*, *Pleuroxus*, *Moina*, *Alona* and Rotifers) were higher in high TP level (Fig 2.6). Free swimming large cladocerans *Polyhemus* and plant associated *Simocephalus* biomasses were very low whereas in lakes with higher TP was mostly composed of typical small sized groups such as *Bosmina*, *Chydorus* and *Moina* as well as rotifers where the list of genus was given at appendix B. Furthermore the zooplankton community in lakes was dominated by rotifers, followed by *Bosmina*.

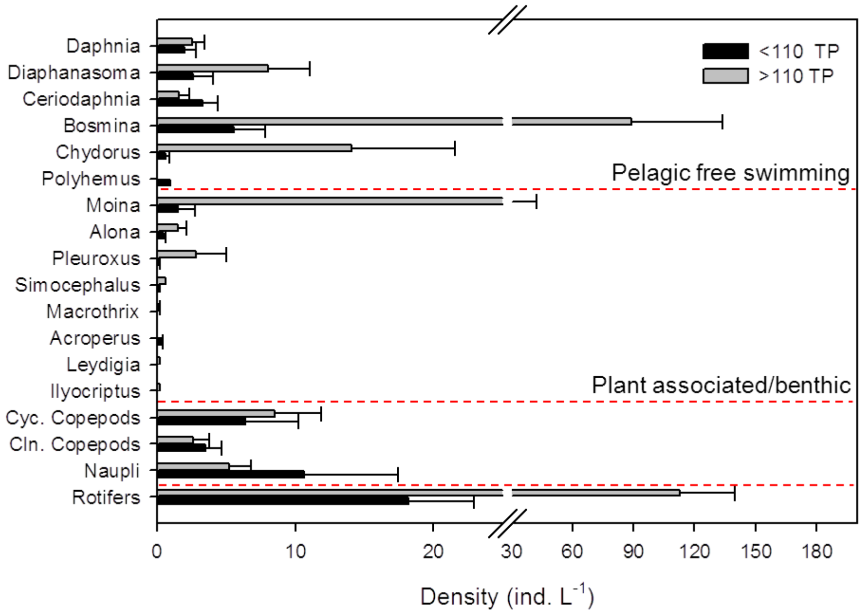


Figure 2.6. Mean density of free-swimming and plant associated/benthic cladocerans, copepods (including both copepodites and adults), naupli (I-IV stage), and rotifers in lakes. The means were given with (±1SE).

In addition, despite there were no significant relationship found between genus richness and latitude, the richness was decrease with increasing salinity (Fig. 2.7.). In the estimation of richness, copepods were used as calanoid, cyclopoid and naupli (I-IV stages) apart from that cladocerans and rotifers used as genus level.

At high salinities, biomass of cladocerans, which consisted of plant associated/benthic *Leydigia leydigi* and free swimming *Chydorus sphericus* with a very low biomass that displayed remarkable decrease.

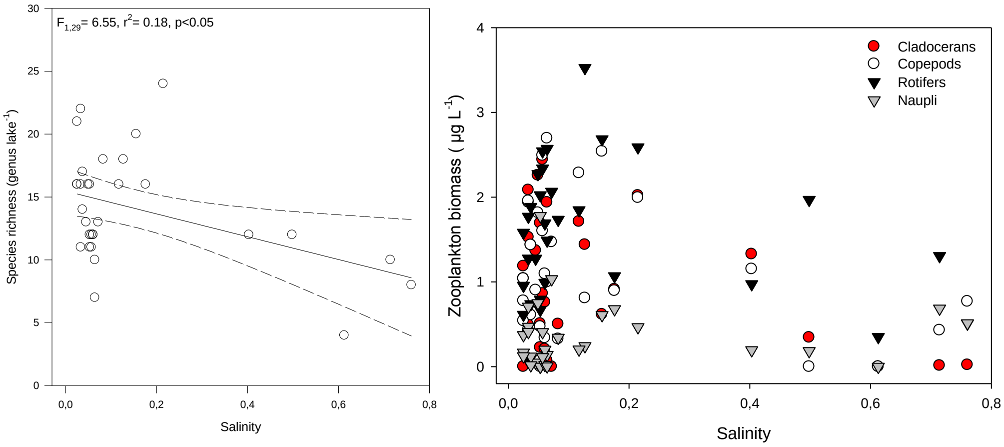


Figure 2.7. a) Species richness of lakes in relation to salinity. Richness was derived from total number of cladocerans and rotifers genus as well as copepods (cyclopoid, clanoid and naupli) in each lake. Solid lines display the regression slope; dashed line display the confidence intervals. b) Biomass of zooplankton in relation to salinity. Note that the salinity scale and zooplankton biomass were given log+1 transformed.

4.3.2. Size and habitat

Multiple regression analysis also confirmed that the small sized individuals both littoral and pelagic zone of lakes were also positively related to the fish density but negatively to the latitude (Fig. 2.8., Table 2.2.). Moreover, the biomass of small sized individuals increased with decreasing latitude which is negatively correlated with salinity. However, the species composition of small sized individuals did not show remarkable difference between high and low latitude. In contrast to small sized, large sized zooplankton did not display significant relation between latitude (see Appendix B).

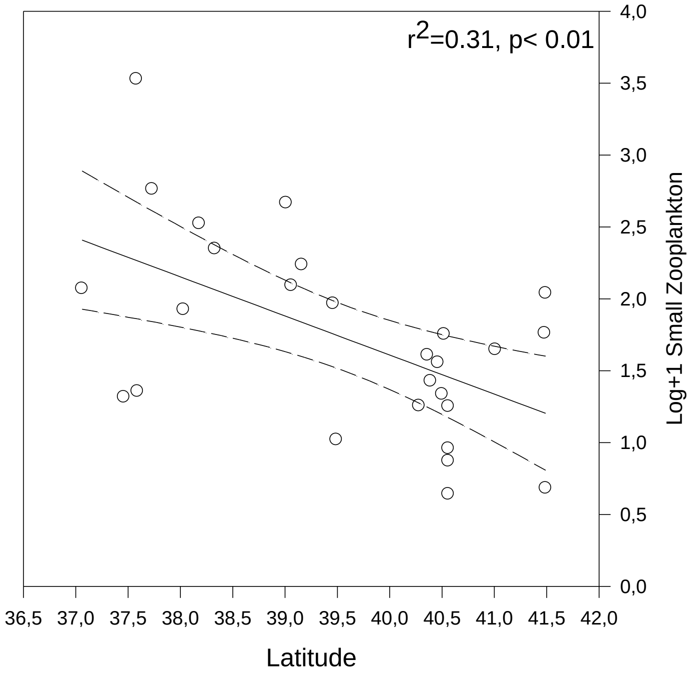


Figure 2.8. Relation between small sized zooplankton and Latitude. Note that scale of small zooplankton fish was log+1 transformed. Solid lines display the regression slope; dashed line display the confidence intervals.

Moreover, small individuals both from littoral and pelagic were increased with increasing fish density. In addition, *Daphnia* were decreased with the increasing fish (Table 2.2.). The zooplankton size diversity did not show a significant respond to the independent variables of total fish. However, as a result of linear regression showed that there was a negative relationship between zooplankton size diversity and small fish (<10cm) which reflects the predation pressure on zooplankton (Fig 2.9.). Furthermore, the size diversity of zooplankton in littoral was also negatively related with fish whilst positively related with latitude.

In addition, the mean body size of the zooplankton biomass displayed critically significant negative relationship with latitude.

Futhermore, the large sized zooplankton was vulnerable to the fish though the density of small sized individuals was found higher above the smoothed curve than the larger ones, which reflects the size dependent predation (Fig. 2.10).

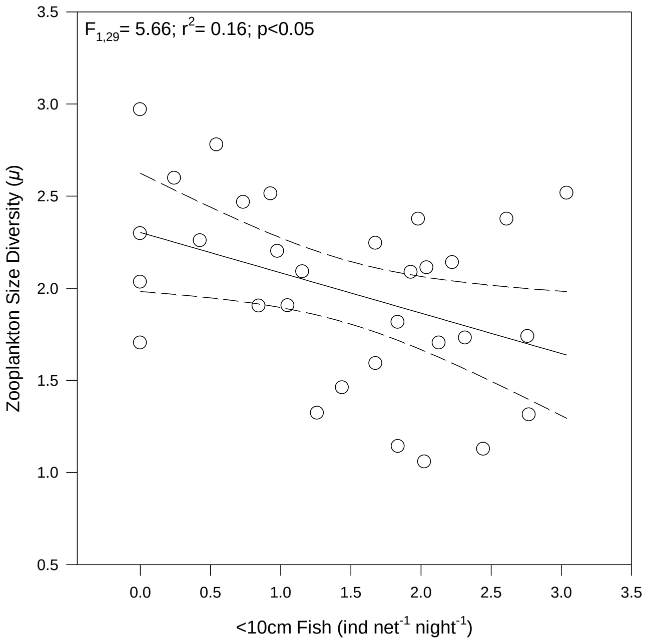


Figure 2.9. Relation between zooplankton size diversity and <10cm Fish in lakes. Note that scale of <10cm fish was log+1 transformed. Solid lines display the regression slope; dashed line display the confidence intervals.

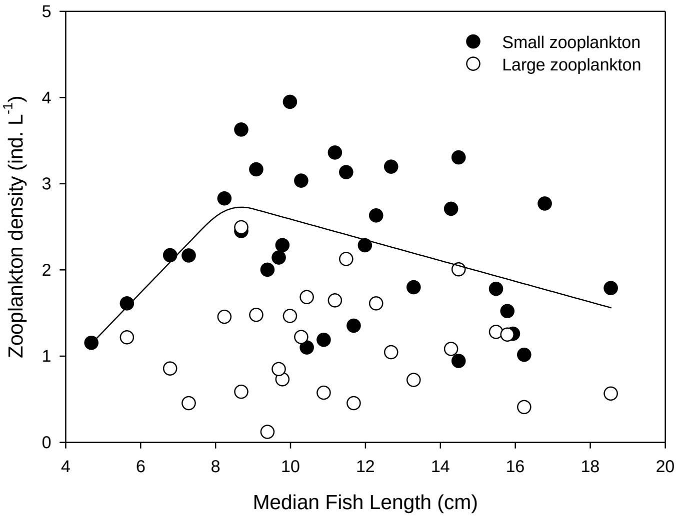


Figure 2.10. Relationship between predator and prey size with smoothed curve. Note that the zooplankton density was log+1 transformed.

2.4.3.Trophic Structure

2.4.3.1. Top-down effects: Fish assemblages

Fourty different fish species were identified in the studied 31 lakes and mostly composed of cyprinids %57.5 (Appendix C). Cobitidae, Gobiidae, Mugillidae, Percidae and Salmonidae were represented by two species whereas the other families (Atherinidae, Balitoridae, Centrarchidae, Cichlidae, Esosidae and Poeciliidae) were represented by only one species.

Although the fish density at the pelagic and littoral zone of lake did not display differences (one-way ANOVA, $F_{1,60}$=3.72; p>0.05), small sized fish (<10cm standard length) which were potential predators was associated with the submerged plant (one-way ANOVA, $F_{1,60}$= 4.66; p<0.05) (Fig. 2.11.).

Furthermore, the results based on multiple regressions confirmed that the mean fish body length was increase with increasing latitude. Hence the large sized fish were found in cooler conditions (see latitude and temperature interaction at Pearson correlation matrix table 2.2.). Furthermore, plankti-omnivor fish:zooplankton ratio was negatively related with latitude which was corresponding to the increase predation pressure on zooplankton under the warmer conditions.

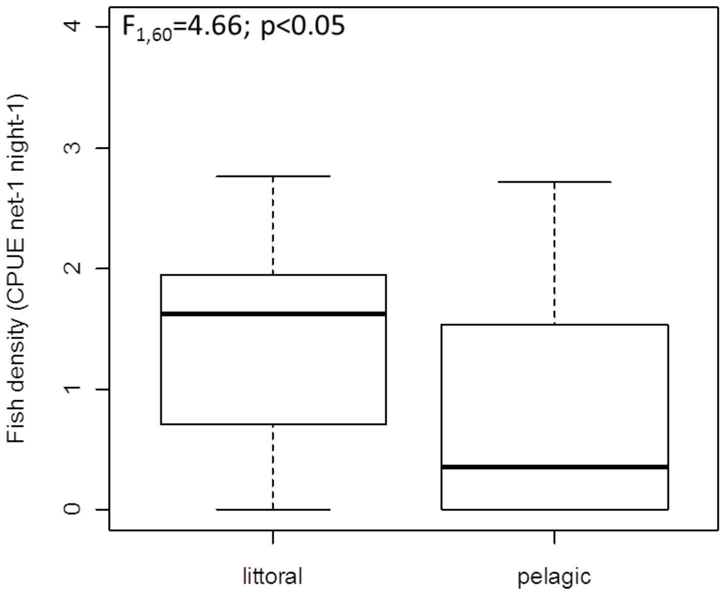


Figure 2.11. Fish density (<10cm standard length) within the habitat. Box plots show the 25%, 50% and 75% percentiles for the habitat. Note that the scale of fish density was log transformed.

2.4.3.2. Bottom-up effects

The results from multiple regression analyses showed that Chl *a*, was positively related with TP however did not display any relation with latitude, PVI % and fish. The piecewise regression analysis confirmed that the concentration of Chl *a*, increased at the 67µg L^{-1} of TP (r^2= 0.48, $p<0.001$) (Fig. 2.12.). Furthermore, the ratio of Chl a: TP and TN:TP was found negatively related with latitude. However, the zooplankton:phytoplankton ratio did not display a clear trend with the independent variables. In addition, planktiomnivor fish:zooplankton ratio was negatively related with TP in contrast to general theory.

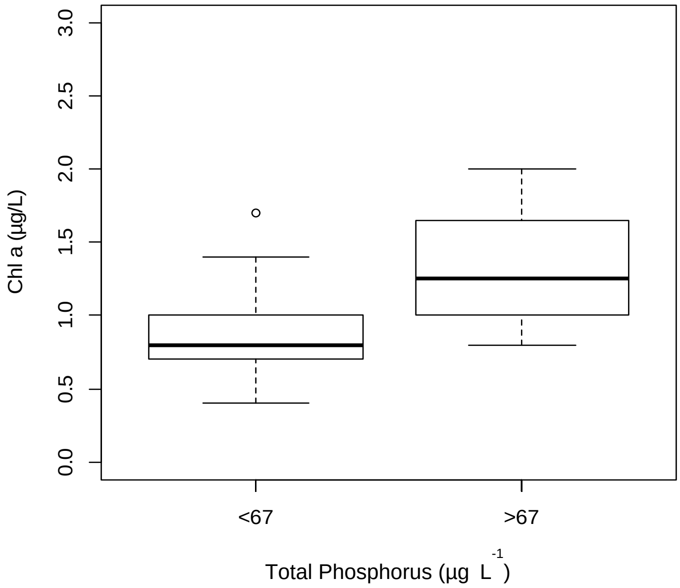


Figure 2.12. The relation between TP and Chl *a*. Note that the scale of Chl *a* was log+1 transformed.

2.5. Discussion

Total phosphorus appears to be the most critical factor for zooplankton community composition, size and habitat distribution and for trophic structure of the lakes. Latitude became important following TP though controlling mostly the size and habitat distribution of zooplankters and the trophic structure but not community composition. Furthermore, size diversity and the biomass of small zooplankton was influence by the fish. Contrary to expectations, submerged plants (PVI %) was the least important independent variable and had no effect on the zooplankton biomass.

For the explanation of community composition and size distribution of zooplankton, total phosphorus, which is a classic bottom-up variable, was the most important independent variable. The effect of TP was not exhibit the same extent for all taxa. Zooplankton biomass including total cladocerans and total copepods particularly cyclopoid copepods were increased with the increasing TP. Becoming a rapid swimmer, Cyclops were take advantage at increasing turbidity (Liljendahl et al., 2008). In contrast to general findings that Daphnia biomass display unimodal distribution (peaks at 0.5 μg P L^{-1}) along TP gradient (Jeppesen et al., 2003), in the present study the zooplankton biomass was display monotonic increase which was consistent with the findings of Gyllström et al. (2005). As a matter of fact that, the monotonic increase of zooplankton biomass with increasing TP probably due to the narrow TP range. Furthermore, increasing TP concentrations in lakes allow the survival of larger individuals possibly as a consequence of low visibility, which create an effective refuge against visual hunting predators (Gonzales Sagrario et al., 2005; Nurminen et al., 2008b, Nurminen et al., 2010). Thus the decreasing planktiomnivor: zooplankton ratio with increasing TP could be related this refuge capability. On the other hand, rotifers did not respond to the changes in TP despite higher density was observed in >110μg L^{-1} TP.

This may be a reason of being also dominant in low TP concentrations. In warm lakes (subtropical and tropical) at low nutrient concentration was also consisted of small zooplankton (Meerhoff et al., 2007b; Havens et al., 2009; Iglesias et al., 2011).

In the present study the zooplankton body sizes decreased with decreasing latitude. Further, size has been declared as the third most important feature for determining the effect of climate change namely temperature (Defaruse et al. 2009). In the present study, small sized individuals (both in littoral and pelagic) were found in warmer lower latitudes. The results were consistent with the previous findings (Moore and Folt, 1993) however Gyllström et al. (2005), a cross comparison from 81 lakes along Europe, suggested that there was no clear evidence on the size structure depending on climate. Although the study conducted in a long distance, there were only 4 lakes below 40 °N and also rotifers were calculated by standard weight thus this might be possible explanation for not detecting the clear trend. However, recent studies have suggested that the reduced zooplankton size structure is as a consequence of high fish predation pressure than temperature that the former strongly increases towards warmer lakes (Meerhoff et al., 2007b; Havens et al., 2009a; Brucet et al., 2010).

Moreover, the fish predator affected the zooplankton community via size selective predation (Fig 4.10). Removal of larger individuals by fish, smaller ones are favored and as larger ones had superiority over smaller ones since the larger ones niche is much wider (Brooks &Dodson, 1965). In addition, fish size composition of lakes was strongly predominated with small fish (<10 cm) and the size diversity of zooplankton became narrower which reflected the strong predation pressure on zooplankton. Moreover, the Planktiomnivore fish: zooplankton ratio was increased towards warmer lakes that showed the strong fish predation in the southern lakes. These findings were concurred with the previous studies that omnivorous fish: zooplankton ratio was observed high in warm lakes in contrast to cold lakes (Gyllström et al., 2005; Meerhoff et al., 2007b; Iglesias et al., 2008; Havens et al., 2009; Teixeira-de Mello et al., 2009; Jeppesen et al., 2010a; Lacerot, G., 2010).

However, the control on phytoplankton by zooplankton was not clear in the present study as probably being dominated by small size individuals which are not efficient grazer of phytoplankton. Furthermore, fish was more in the littoral that is consistent with previous findings which were indicated that fish are associated with plant in warm lakes however the researches were mostly from subtropics and a Mediterranean lake (Meerhoff et al., 2007a; Teixeira-de-Mello et al., 2009; Castro et. al, 2007).

Thus zooplankton did not use submerged plant as a refuge against predation due to the aggregation of fish among vegetation (Fig 2.11.).

Thus the behavioral response of zooplankton against fish predation might not be similar to the temperate lakes as they are not using macrophyte as a refuge in warmer lakes. Accordingly, zooplankton underwent diel vertical migration in warm lakes in contrast to temperate shallow lakes that elucidated from both in field surveys (e.g. subtropics: Meerhoff et al., 2007a; Mediterranean: Castro et al., 2007, Tavşanoğlu et al., in prep.) and in laboratory experiments (e.g. subtropics: Meerhoff et al., 2006; Tavşanoğlu et al., 2012).

There are also some evidences on the changes of zooplankton size structure along salinity gradient (Jeppesen et al., 2007; Brucet et al., 2009; Jensen et al., 2010). In the present study, zooplankton richness was decreased with increasing salinity and eventually small sized individuals (rotifers and small cladocerans) were found dominant. The results were also concurs with the previous findings that the community composition shift from large cladocerans to copepods and small cladocerans in brakish lakes (Brucet et al., 2009; Jensen et al., 2010). Moreover, negative relationship between salinity and species richness were consistent with the previous studies (Williams et al., 1990; Schallenberg et al., 2003; Brucet el al., 2009; Jensen et al., 2010; Viajeh and Spoljar, 2012). On the other hand, Kaya et al, (2010) suggested that there were a positive relationship between salinity and species richness in Turkish inland water.

However, authors stated that there were some points to take into accounts such as excluding cladocerans and copepods instead of rotifers and sampling were performed in few points.

With the climate warming perspectives, present study suggested that total phosphorus may influences the zooplankton assemblages towards small sized individuals beside the impacts of higher predation pressure of small fish. Furthermore, zooplankton size was also decreased with increased salinity. The biomass of cladocerans displayed remarkable decrease whilst rotifers were higher than that of. Moreover, not only size but also richness was decreased increasing salinity. Furthermore, considering the predictions of global climate change on the Mediterranean region which states that ongoing warming may trigger the severe drought (drop water level), salinization (high evaporation) and eutrophication despite the reduction of external loading. Thus, together with the finding from present study and expectations from predictions, the zooplankton assemblages in lakes located in Anatolia will face to severe impacts through predation by small fish and increased nutrient. Accordingly, with the high abundance of small fish and reduced phytoplankton grazing by zooplankton thereby will cause more eutrophic conditions near feature.

CHAPTER 3

DIEL MIGRATION PATTERN AND SIZE STRUCTURE OF ZOOPLANKTON IN TURKISH SHALLOW LAKES

3.1. Introduction

Zooplankton assemblage and size structure are influenced by fish predation (Brooks & Dodson, 1965), particularly in shallow lakes (Jeppesen et al., 2004). The predation pressure is the key importance for a heterogeneous distribution of zooplankton (Burks et al., 2002) as the zooplankton develop efficient defence mechanisms against predators, for instance by aggregating among submerged plants during day and moving to the open water during night, known as “diel horizontal migration” (DHM) (Lauridsen & Lodge, 1996; Burks et al., 2001); or by dwelling near the bottom or in deep waters during the day and ascending to the surface at night, termed “diel vertical migration” (DVM) (Gliwicz, 1986; Dodson, 1990). So far, most DHM studies have been undertaken in north temperate shallow lakes (Burks et al., 2002), whereas most DVM studies derive from deep lakes (e.g. Gliwicz, 1986; Lampert, 1989; Dodson et al., 1997; Winder et al., 2003). Recent studies have shown that the migration pattern of zooplankton differs between cold temperate and warmer lakes (e.g. subtropical lakes, Meerhoff et al. (2006, 2007a), and Mediterranean lakes, Brucet et al. (2010), probably reflecting the higher aggregation of small and high fish density within macrophyte beds in the warmer lakes, which weakens the role of submerged plants as a daytime refuge for zooplankton (e.g. subtropical lakes, Meerhoff et al., 2006, 2007a, and Mediterranean lakes, Brucet et al., 2010). In accordance, a recent laboratory experiment provides evidence that sediment but not plants are used as refuge against fish predation in Mediterranean lakes (Tavşanoğlu et al. 2012).

Furthermore, the fish community of warm lakes is dominated by omnivorous feeding, small sized and frequent reproducing species (Gonzalez-Bergonzoni, 2012; Jeppesen et al, 2010a; Teixera de Mello et al., 2009) that exert a high predation pressure on the zooplankton (Jeppesen et al, 2010b). Moreover, fish predation also has notable effects on the size structure of the zooplankton, as fish select large-bodied species and individuals (Brooks & Dodson, 1965). Thus higher fish predation will affect the size structure of zooplankton which exhibits a size shift from large size to small (Brucet et al., 2010, 2011). However, until now only few studies have investigated the predation effects on the whole migrating zooplankton size structure shifts among submerged plant and open water. Furthermore, studies addressing zooplankton size structure often neglected small sized rotifers which are also sensitive to environmental changes (May & O’Hare, 2005).
To the best of our knowledge, no study has so far assessed how zooplankton size structure and their diel movements are changing in different habitats (plant and open) for Mediterranean shallow lakes.

We hypothesized that the size structure and diel aggregation of zooplankton were altered with increasing fish predation, and macrophyte was not an effective in providing refuge for zooplankton as largely being habitat for fish. Furthermore habitat choice of larger sized migrating zooplankton would change according to the predator assemblage and distribution. Thus, we expected lakes to be mostly dominated by small-sized zooplankton and a higher occurrence of DVM.

3.2. Material and methods

3.2.1 .Design and sampling methodology

Turkey is located between the temperate and the subtropical zone and is therefore exhibits by different climate conditions (Şekercioğlu et al., 2011). According to the Köppen-Geiger classification system, the Mediterranean climate prevails in most parts of the country; however, maritime temperate, warm summer continental and large steppe climates are also represented (Şekercioğlu et al., 2011). We selected eleven permanent shallow lakes from 41ºN to 37ºN. The artificial plant bed experiment was performed during the summer period (Table 3.1) in the eleven lakes where three artificial plant beds enclosure experimental set were placed, mimicking submerged plants in the littoral zone (using the method of Meerhoff et al. (2007a), with minor modifications).

Table 3.1. Main physical, chemical and biological characteristics of the eleven study lakes. TP: Total phosphorus; TN: Total Nitrogen; Chl *a*: Chlorophyll a; CPUE: Catch per unit effort (ind. net^{-1} night^{-1}); PVI: plant volume inhabited; Temp: Air Temperature. *Thirty years of Average air temperature for August (the sampling month).

Variables	**Hamam**	**K. Akgöl**	**Taşkısığı**	**Yeniçağa**	**GölcükB**	**Eymir**	**Mogan**	**Emre**	**Karagöl**	**GölcükÖ**	**Saklı**
Latitude	41.5	40.5	40.5	40.5	40.4	39.5	39.4	39.1	38.3	38.2	37.5
Mean Depth (m)	1.5	0.7	2.2	1.9	1.6	1.0	0.7	1.1	2.0	1.5	4.8
*Temp. (°C)	22.7	22.8	22.8	19.6	19.6	22.6	22.6	21.6	25.7	26.8	24.2
Secchi Depth(m)	0.40	0.20	0.50	0.90	1.90	1.0	0.50	0.80	0.20	0.25	1.42
Salinity (‰)	0.06	0.14	0.15	0.16	0.08	1.90	2.41	0.13	0.14	0.12	0.50
Chl *a* (µg L^{-1})	19.3	60.7	36.7	7.68	4.82	6.5	15	24.5	28.6	14.5	4.54
PVI %	6.8	0	0	7.48	14.2	2.65	64.3	13.0	0	0	0.03
TP (µg L^{-1})	60.1	632	89.7	266	52.5	240	153	88	246	326	19
TN (µg L^{-1})	939	2096	1349	731	613	2180	1279	1803	1796	2028	1014
Fish CPUE	89	644	318	148	48	103	332	108	88	50	9

The artificial plant beds consisted of 1-m diameter plastic rings with an attached fishing line from which the artificial plants, resembling *Elodea canadensis*, were hung (Fig. 3.1). Plant volume inhabited (PVI%, sensu Canfield et al, 1984) of each module was ca. 70%, the plants being 0.8-1.0 m long. Before sampling we left the module to acclimatize for 10 hours.

Figure 3.1. Artificial plant beds.

We took water samples for chemical analysis (total phosphorus, total nitrogen, chlorophyll *a*) and determination of *in situ* parameters with a tube sampler in the open water. Water transparency was measured with a 20 cm diameter Secchi disc.

Daytime and night-time zooplankton samples were taken from each artificial plant module (hereafter termed ‘plant’: ‘P’) and at each open water site (‘O’, sites without plants) from the surface to a few cm above the sediment using a tube sampler. The water (ca. 10 L) was collected at five different spots coring the inside within each module, mixed in a barrel, filtered through 20 μm mesh size filter and preserved in Lugol’s solution (4%). To avoid sediment resuspension, samples were taken from a boat.

We identified all zooplankton taxa to genus or species level and counted 50-100 individuals of the most abundant taxa. Copepods were separated into cyclopoids, calanoids (including adults and copepoditites) and nauplii. We classified *Daphnia* and *Simocephalus* as large bodied and, *Bosmina, Chydorus, Alona, Pleuroxus, Moina, Ceriodaphnia,* and *Diaphanasoma* as small-medium bodied cladocerans. We measured body size of around 25 individuals of each taxon whenever possible and calculated body weight from length using published relationships from the literature (Dumont et al., 1975; Bottrell et al., 1976; McCauley, 1984; Michaloudi, 2005). We converted the biovolume of rotifers to dry weight according to Dumont (1975); Ruttner-Kolinsko (1977) and Malley et al. (1989). *Chaoborus* were sampled using a tube sampler (10L) and classified as ‘absence’ and ‘presence’.

We performed fish sampling with Lundgrens multi-mesh gill nets (length 30 m; height 1.5 m; 12 panels with mesh sizes (knot to knot) of 5.0, 6.25, 8.0, 10.0, 12.5, 15.5, 19.5, 24.0, 29.0, 35.0, 43.0 and 55.0 mm) depending on lake size. The nets were set overnight both parallel to and approximately a few metres away from the plants and in the open water zone of the lake for an average duration of 12 hours. Fish were counted, measured (total length) and weighed (fresh mass). Based on literature data, we categorized fish as planktivorous and piscivorous (http://www.fishbase.org).

This study has funded by TUBITAK 105Y332; TUBITAK 110 Y 125, METU-BAP (BAP-07-02-2010-00-01) and REFRESH (EU-FP7-20091). The physical, chemical and biological data excluding zooplankton were taken from Beklioğlu et al.,(in prep.). Thus the data excluding zooplankton will have used in the PhD thesis who have carried out their thesis at METU, Limnology Laboratory (Ayşe İdil Çakıroğlu, Eti Ester Levi, Gizem Bezirci, Şeyda Erdoğan) as well as completed PhD thesis (Arda Özen).

3.2.2..Laboratory Analyses

Samples for chemical analysis were frozen until analyses. For total phosphorus (TP), the acid hydrolysis method was used (Mackereth et al., 1978). For total nitrogen (TN) analysis Scalar Autoanalyzer Method was used (San++ Automated Wet Chemistry Analyzer, Skalar Analytical, B.V., Breda, Netherlands). The chlorophyll a was determined using ethanol extraction (Jespersen & Christoffersen, 1987) and the absorbance measured at 663 and 750 nm.

We calculated size diversity for each zooplankton replica following Quintana et al. (2008). The proposed size diversity (μ) is computed based on the Shannon diversity index adapted for a continuous variable, such as body size. This measure takes the form of an integral involving the probability density function of the size of the individuals described by the following equation: where $p_x(x)$ is the probability density function of size x. Nonparametric kernel estimation was used as probability density function after data standardization using division of sample data by their geometric mean value. We calculated the average size diversity of the three replicas in each habitat (open, plant) and for each time (day and night).

$$\mu = {}_{0}^{+\infty} p_x \; x \; log_2 p_x \; x \; dx$$

3.2.3. Statistical Analysis

We used two-way ANOVA to detect significant differences of zooplankton density for two main factors: ‘habitat’ (open, plant) and ‘time’ (day, night). Classification of the DHM pattern was based on the significant interaction ‘habitat’ x ‘time’ in the ANOVA where the density of zooplankton decreased during night among the submerged plants and simultaneously increased slightly in the open water. Classification of DVM was based on the significant effect of ‘time’ in the ANOVA where the density of zooplankton increases in all habitats at night. The contrasting patterns mentioned above were classified as ‘reverse’ (RHM, RVM). Furthermore, we conducted separate General Linear Model analyses (unbalanced ANOVA) to show if there is any differences in the abundance of migrating zooplankton between different size classes and time within open and plant sites. Linear regression analyses were performed to investigate the relationship between fish density and zooplankton size diversity as well as habitat preference of fish along the latitude.

We transformed ($\log_{10}(x+1)$, $\log_{10}$) the data to fulfill the requirements of homoscedasticity and normality of residuals. Holm Sidák *post hoc* tests were used. The analyses were performed using Statistica10.Trial version (Stat Soft Inc., Tulsa, USA).

3.3. Results

3.3.1. Physicochemical characteristics of Lakes

The results of water samples during sampling periods showed variations in the major physicochemical parameters in lakes that have been given Table 3.1. The Secchi depth, which is an indicator of water transparency, was observed very low among lakes except Lakes GölcükB and Saklı. Furthermore, the low transparent lakes had no submerged plant (0 PVI %) while TP and TN of these lakes were high ranging from 1349-2096 µg L^{-1}. Moreover the lake (Küçük Akgöl) with highest nutrient had also very high fish density and Chl *a*. Salinity lies ranging from 0.06 to 2.41 ‰ however the gradient was very narrow.

2.3.2. Diel and spatial aggregation of zooplankton taxa

The community composition was mostly dominated by small sized cladocerans, rotifers and copepods in lakes except Lakes GölcükB, Eymir, and Mogan (Fig. 3.2). Particularly the slightly saline lakes (Lake Eymir and Mogan) consisted of calanoid copepods, rotifers and large sized cladocerans (Fig. 3.2). Furthermore the geometric mean of the taxa was not varying both in habitat and time in lakes (Fig. 3.2). However, the abundance of zooplankton communities in the habitats (open and plant) differed between day and night.

We found evidences of vertical migration in lakes. Lake Hamam, mainly consisted of small-sized individuals and plant-associated/benthic *Moina* performed diel horizontal migration (reverse) (two-way ANOVA, interaction between ‘time and habitat’, $p<0.001$) (Table 3.2). In Lakes GölcükB and Saklı, both of which had narrow size class range, the density of free-swimming cladocerans was significantly higher in the night-time (two-way ANOVA, ‘time’ effect, $p<0.05$) (Table 3.2). In Küçük Akgöl, *Moina* was the only migrating species that underwent reverse vertical migration (two-way ANOVA, ‘time’ effect, $p<0.05$).

In Lake Eymir, the density of free-swimming cladocerans, *D. magna* was also significantly higher in the night-time (two-way ANOVA, ‘time’ effect, *p*<0.05), but the size class range was wider than that of other lakes (Fig 3.2).

We found significant migration patterns for copepods only in a few study lakes though calanoid copepods display only vertical migration (Table 3.2).

In Lakes Mogan and Emre the densities of free-swimming cladocerans, plant-associated/benthic cladocerans, copepods and rotifers (*Filinia* in Lake Mogan and *Asplanchna* in Lake Emre) were higher during the day, i.e., reverse vertical migration was observed (two-way ANOVA, ’time’ effect, *p*<0.05; Table 3.2, Fig. 3.2). Plant-associated/benthic cladocerans occurred in very low numbers and no clear pattern probably reflecting the absence of periphyton resulting from the short term incubations of the experimental set up, could be discerned, except for Lakes Mogan and Emre where reverse migration occurred. Moreover, despite the fact that diel changes in rotifer migration in shallow lakes were assessed in limited number of studies, we found significant vertical migration for the some rotifera species which included *Brachionus*, *Anureopsis* and *Polyarthra* that displayed significant diel vertical migration (two-way ANOVA, ‘time’ effect, *p*<0.05), while *Asplanchna* displayed reverse vertical migration (Table 3.2). However *Filinia*, *Hexarthra* and *Trichocerca* displayed both reverse and vertical migration varying with the lakes (Table 3.2).

Furthermore, in Lake Yeniçağa, we found diel horizontal migration (reverse) only for free-swimming cladoceran *Ceriodaphnia* (two-way ANOVA, interaction between ‘time and habitat’, *p*<0.001); however, no clear trend could be identified for other groups. Whereas in Lake Karagöl where the size range was very narrow and mainly held small-sized rotifers was not display significant migration pattern (two-way ANOVA, *p*>0.05) (Fig. 3.2).

Thus, most of the zooplankton taxa showed differences during day and night between open water and plant sites (Fig. 3.2) and particularly displayed vertical migration both direct and reverse. While horizontal migration was detected only for *Ceriodaphnia*, *Moina* and Cyclopoid copepods. However in overall total cladocerans performed migration than that of total copepods and rotifers in lakes.

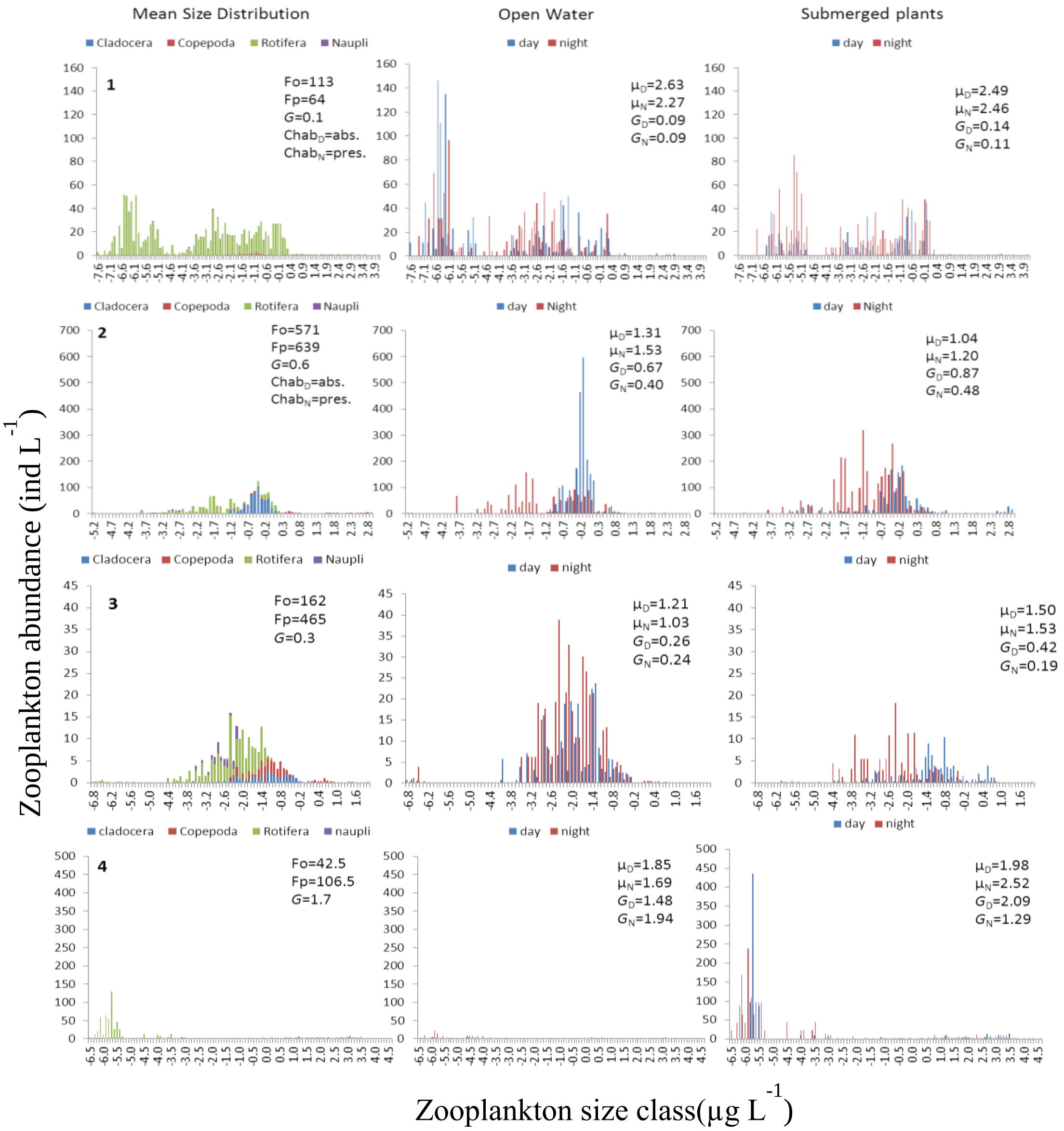
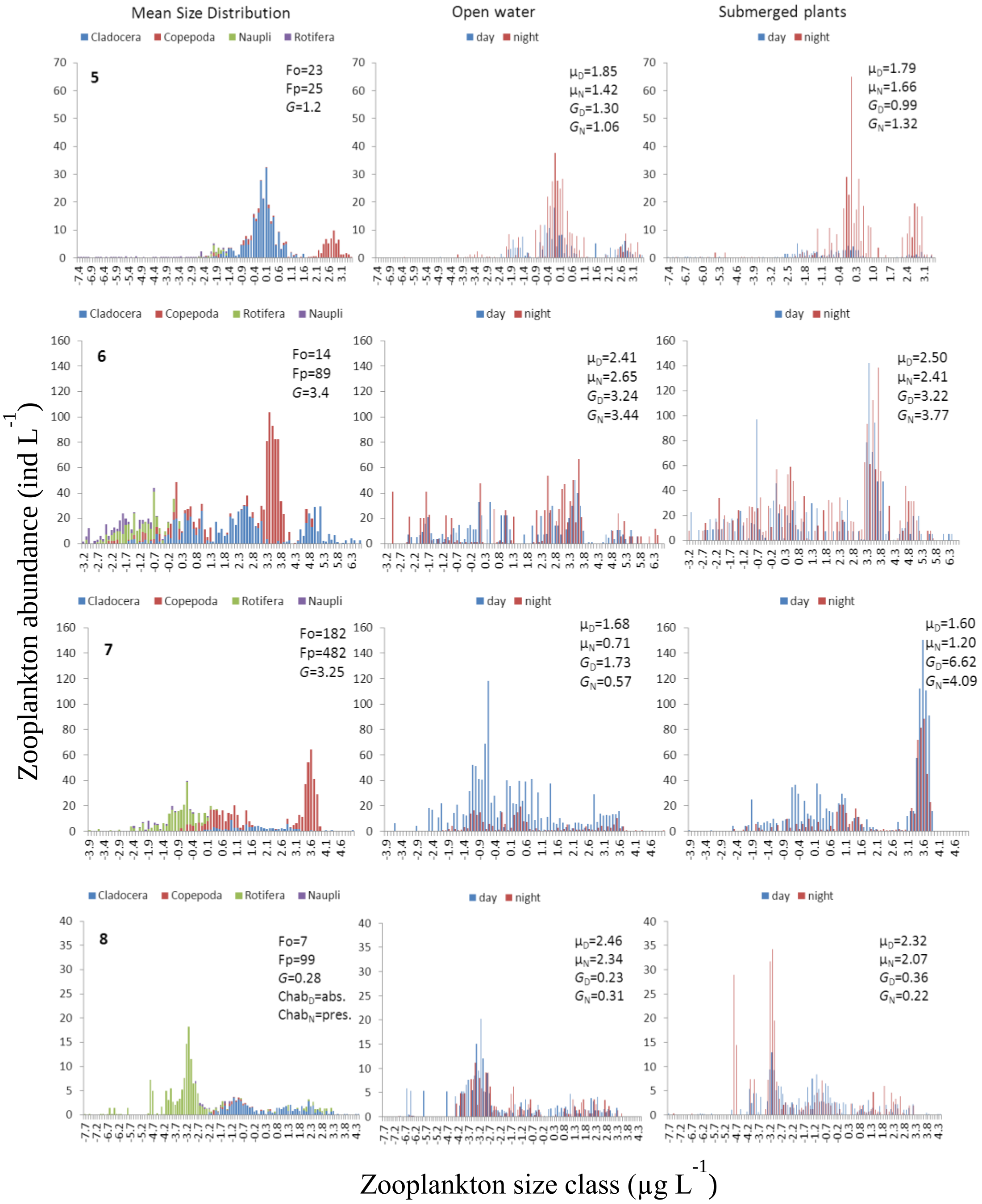


Figure 3.2. Mean zooplankton size distribution for each lake in open and plantsites during day and night. *G*, geometric mean of zooplankton size; μ_D= size diversity during day; μ_N=size diversity during night; G_D= geometric mean during day; G_N= geometric mean during night.Fo= mean fish densith in open water; Fp= mean fish density in plan (ind net^{-1} night^{-1}). 1: Lake Hamam; 2: Lake Küçük Akgöl; 3: Lake Taşkısığı; 4: Lake Yeniçağa; 5: Lake GölcükB; 6:Lake Eymir; 7: Lake Mogan; 8: Lake Emre; 9: Lake Karagöl; 10:Lake GölcükÖ; 11: Lake Saklı Note the different scale in each lake.



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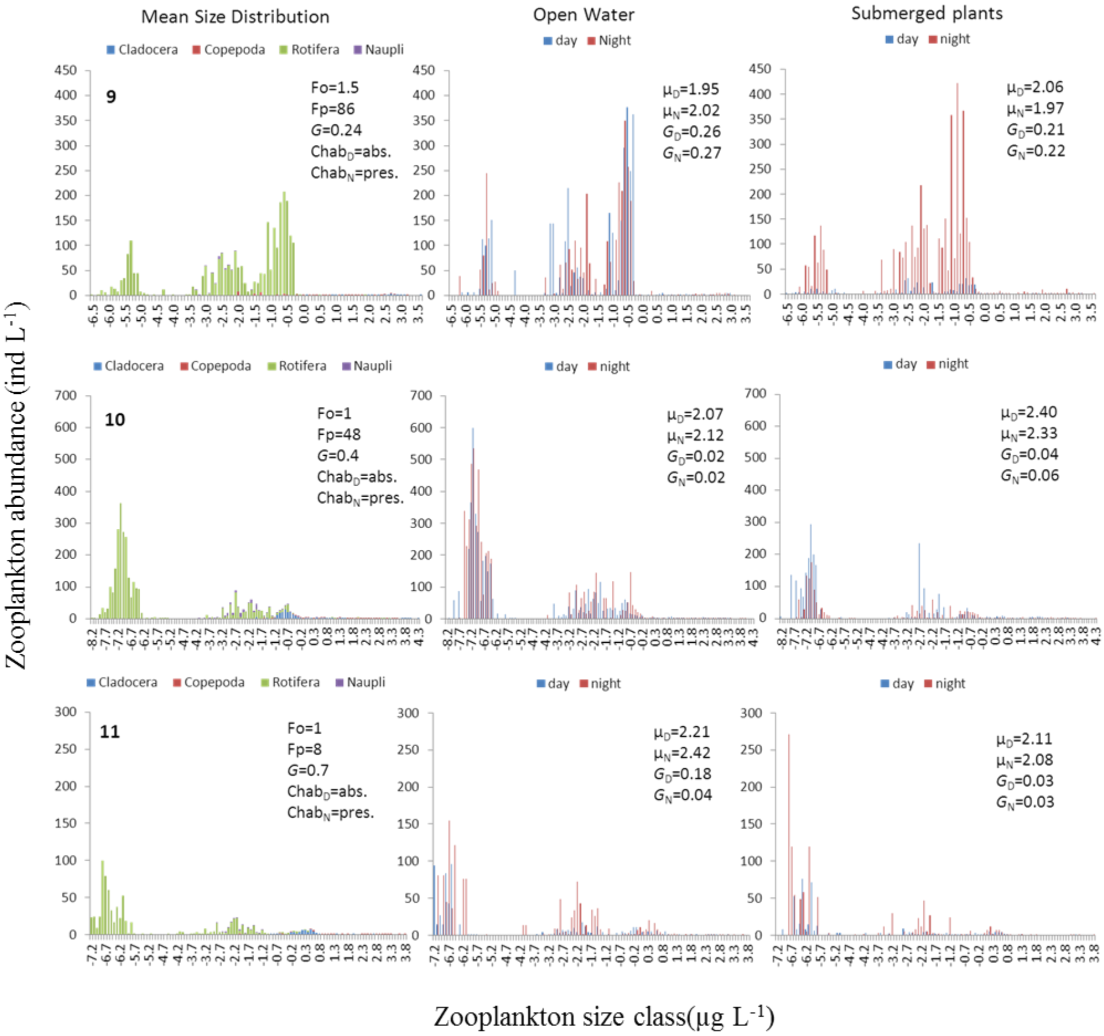

Figure 3.2. Continues.

Table 3.2. Migration pattern of the zooplankton groups among eleven lakes. Only significant results according to the two-way Anova test are presented. Symbols: DVM, diel vertical migration; DHM: diel horizontal migration; RVM: reverse vertical migration; RHM: reverse horizontal migration. no: no migration; - : too few numers for statistical tests or no species present.

	Hamam	**Küçük Akgöl**	**Taşkısığı**	**Yeniçağa**	**GölcükB**	**Eymir**	**Mogan**	**Emre**	**Karagöl**	**GölcükÖ**	**Saklı**
CLADOCERA											
Tot. clad.	rhm	no	no	rhm	dvm	dvm	rvm	no	no	no	no
Daphnia	-	-	-	no	no	dvm	-	no	no	no	-
Diap.	-		no	-	dvm	no	rvm	-	-	no	-
Cerio.	-	-	-	rhm	dvm	-	-	rvm	-	-	dvm
Moina	rhm	rvm	-	-	-	-	rvm	-	-	-	-
Alona	-	no	-	-	-	dvm	-	-	-	-	-
Bosmina	-	no	-	-	dvm	no	-	no	-	no	-
Chyd.	-	no	no	-	-	dvm	-	rvm	-	-	-
COPEPODA											
Tot.cop.	no	no	no	no	no	no	rvm	rvm	no	no	no
Cln. cop.	-	-	-	no	dvm	no	rvm	-	-	dvm	no
Cyc.cop.	-	rvm	rhm	no	-	-	-	-	-	dhm	-
ROTIFERA											
Tot. rotif.	no	no	dvm	no	-	no	no	no	no	no	dvm
Anureop.	dvm	-	-	-	-	-	-	no	-	no	dvm
Brach.	-	no	dvm	-	-	-	no	-	no	no	dvm
Filinia	-	dvm	dvm	-	-	-	rvm	no	no	no	-
Hexart.	dvm	dvm	-	-	-	no	rvm	no	-	-	no
Polyart.	dvm	dvm	-	no	-	-	-	no	-	no	-
Tricho.	dvm		dvm	-	-	-	-	-	no	rvm	no
Asplan.	-		-	no	-	-	-	rvm	-	-	-

3.3.3. Size Structure of migrating zooplankton

Daphnia displayed diel migration only in Lake Eymir (Table 3.2). Size of the *Daphnia* was not significantly different within the habitat during day, but during night size become larger in open water (GLM ANOVA, $F_{1,79}$= 9.61, $P<0.05$) (Table 3.3). In Lake Eymir, *Daphnia* size was measured between 1.2 and 2.9 mm, however migrating size class range was found >1.4mm (GLM ANOVA; $F_{6,30}$=12,47; $p<0.0001$) in open water whereas in submerged plant the difference of size classes range between day and night was not significant (Fig. 3.3., b). Moreover in the lakes without diel migration, the size ranges of *Daphnia* species were found to be between 0.5-1.7mm (Fig. 3.3.). Although *Daphnia* did not display diel migration in Lake Yeniçağa, considering the whole abundance without separation of sizes, the size class of 1.0-1.8 mm individuals was found high abundance during night at the open water (GLM ANOVA; $F_{1,16}$=4,23; $p<0.05$) (Fig. 3.3., d). Night/ day ratio of size classes in other lakes were similar but there were not found any significant pattern of migration. On the other hand, larger sized (0.9±0.1mm) *Daphnia* was found in open water despite no migration was detected in Lake Emre (GLM ANOVA, $F_{1,\ 130}$=9.98, $P<0.05$) (Fig. 3.3., c). In addition, despite *Daphnia* found in similar size classes in other lakes, the abundance of individuals in each size classes did not large enough to analyses the pattern.

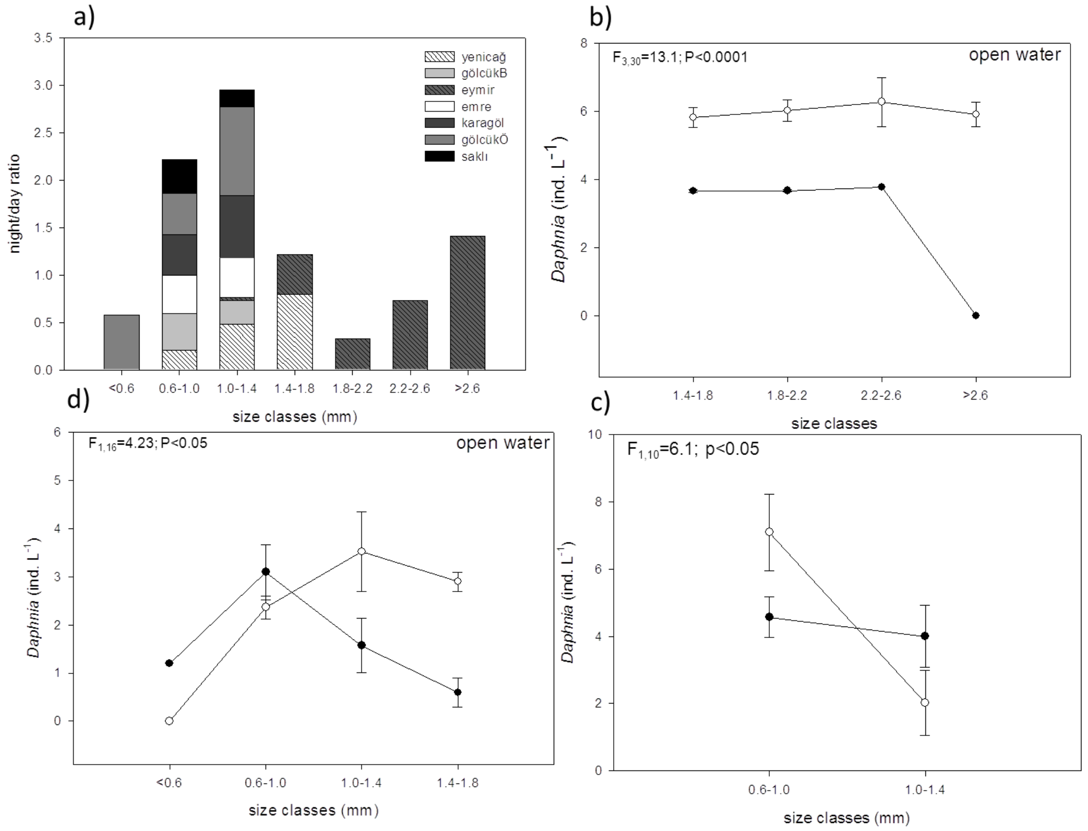

Figure 3.3. Size distribution of *Daphnia*. a) night/day time ratio of *Daphnia* at different size classes in lakes; b)density of *Daphnia* at different size classes in Lake Eymir during day and night within open water; c) density of *Daphnia* at different size classes in Lake Emre; d) density of *Daphnia* at different size classes in Lake Yeniçağa during day and night within open water. Black circle: day; open circle: night.

The diel migration of *Diaphanasoma* was observed in Lake GölcükB (vertical) and Lake Mogan (reverse vertical). In GölcükB, size of the *Diaphanasoma* was similar among habitats (GLM ANOVA, $p>0.05$), but in each size classes the density of individuals were higher during night (GLM ANOVA; $F_{2,48}=6,64; p<0.003$) in open water (Fig 3.4.,a) while in plant, the size classes did not display significant difference. Thus the species performed vertical migration at the >0.4mm in size which was correspond to the range of -1.3 to 0.7 μgL^{-1} (Fig. 3.2.). However, even the largest *Diaphanasoma* was relatively small in comparison to the size of the individuals recorded in Lake Mogan (0.82±0.14mm) where the larger sized were found in open water (GLM ANOVA; $F_{1,94}=14.4$, $P<0.001$) but not display differences among size classes and Lake Eymir (0.95 ±0.17mm). Although the migration of *Diaphanasoma* was not observed in Lake Eymir, the number of large sized individuals found in open water during the day was critically significant (GLM ANOVA; $F_{1,65}=3.68$, $P<0.1$)(Table 3.3).

Despite performing diel migration in lakes, larger size of the *Ceriodaphnia* (≥0.5mm which was correspond to >0.8 µgL-1 in Fig. 3.2.) was observed in open water during the night only in Lake Saklı (GLM ANOVA; $F_{2,44}=4.12$, $P<0.05$) (Fig 3.4.,b) while in GölcükB the larger individual were found during night (habitat time, $F_{1,137}=3.15$; $p<0.1$)(Table 3.3). In other lakes size of the *Ceriodaphnia* did not display significant difference neither spatially nor temporally ($p>0.05$).

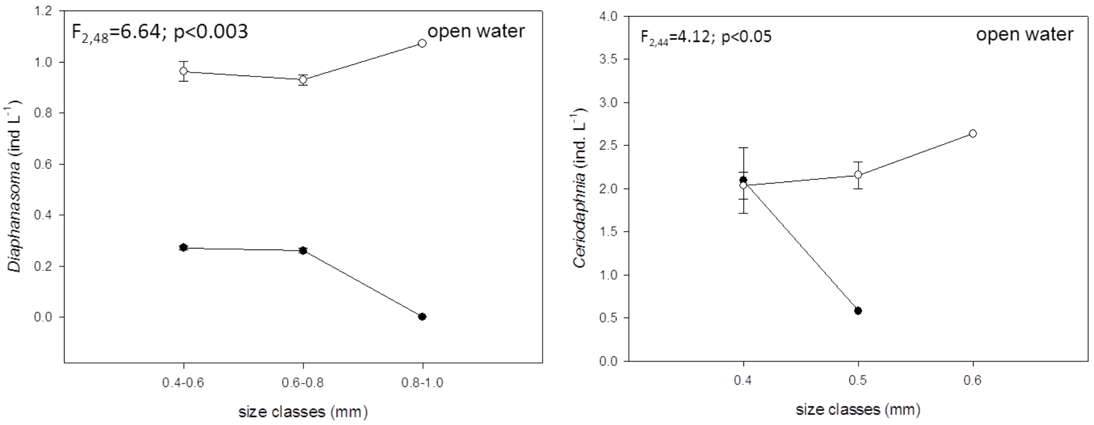

Figure 3.4. Size distribution of free-swimming cladocerans a) *Diaphanasoma* in Lake GölcükB; b) *Ceriodaphnia* Lake Saklı. Black circle: day; open circle: night.

Alona, *Chydorus* and *Bosmina*, which was performed vertical migration in Lakes Eymir, Emre and GölcükB (Table 3.3), had very narrow size range from 0.2 to 0.4 mm (correspond to -2.0- -0.4 μgL^{-1} in Fig 3.2) (Fig. 3.5). On the other hands, despite no migration was performed by *Alona*, *Chydorus,* and *Bosmina* in Lake Küçük Akgöl, the larger sized *Alona* were found to be in open water during day and found in plant during night (GLM ANOVA; $F_{1,19}=5.6$, $P<0.05$), whereas larger sized *Chydorus* was found in plant during day whilst the larger individuals was observed in open water during night (GLM ANOVA; $F_{1,85}= 12.5$, $P<0.05$). Furthermore, larger sized *Bosmina* was found during night in Lakes GölcükB, Küçük Akgöl and GölcükÖ (GLM ANOVA; $F_{1,38}=6.4$, $P<0.05$; $F_{1,106}=7.46$, $P<0.05$, and $F_{1,109}=16.9$, $P<0.001$, respectively).

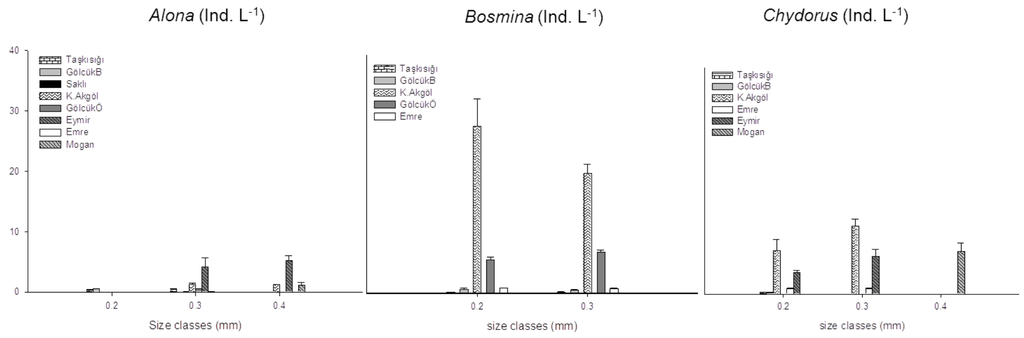

Figure 3.5. Mean density (ind. L^{-1}) with standard error (SE) of size distribution for *Alona*, *Bosmina* and *Chydorus* in lakes. Note same scale in each species.

Moina performed both reverse vertical and horizontal migration in lakes (Table 3.3). *Moina* was larger (0.45±0.18 mm) in open water (GLM ANOVA; $F_{1,77}$=0.69, p<0.01)(Table 3.3) in Lake Hamam whereas in Küçük Akgöl where the habitat did not differ (habitat; $F_{1,90}$= 0.004; p>0.1), larger sized (0.56±0.19 mm) were found during day (GLM ANOVA; $F_{1,90}$=12.92; P<0.001)(Table 3.3). Moreover, in Lake Mogan, size of the *Moina* did not display significant difference.

Although copepods performed diel migration, size structure neither within habitat nor time showed significant difference in lakes (p>0.05). Among migrating rotifers, the size classes of migrating species did not vary (Fig. 3.2) however size classes displayed differences within habitat. Larger sizes of *Anureopsis* (GLM ANOVA; $F_{1,53}$=16.9, *P*<0.001) and *Brachionus* (GLM ANOVA; $F_{1,15}$=5.42, *P*<0.05) in Lake Saklı; *Brachionus* (habitat, $F_{1,47}$=10.2, *P*<0.01) in Lake Taşkısığı and *Hexarthra* in

Lake Küçük Akgöl were found within plant while larger *Filinia* (GLM ANOVA; $F_{1,112}$= 5.47, p<0.05) in Lake Taşkısığı, was observed in open water (Table 3.3).

Furthermore larger sized *Filinia* in Lake Mogan and *Brachionus* in Lake Küçük Akgöl were observed during the day (GLM ANOVA; $F_{1,84}$=9.6, *P*<0.05 and F1,102=15.47, p<0.0001, respectively). However, In Lake Emre, *Asplanchna* that underwent reverse vertical migration, was larger (0.3 ±0.03mm) during the day within plant (GLM ANOVA; $F_{1,27}$=4.33, *P*<0.05) (Table 3.3).

Table 3.3. GLM ANOVA results of size distribution for the migrating zooplankton groups among eleven lakes within plant and open water. Symbols: H:Habitat; T: Time, ns:non-significant. Results were represented as †<0.1; *<0.05; **<0,01;***<0,001. *Alona* and Cyc. copepod excluded due to non significant.

		Hamam	**K. Akgöl**	**Taşkısığı**	**Yeniçağa**	**GölcükB**	**Eymir**	**Mogan**	**Emre**	**Karagöl**	**GölcükÖ**	**Saklı**
Daphnia	H				ns	ns	**		*	ns	ns	ns
	T				ns	ns	ns		ns	ns	ns	ns
	H x T				ns	ns	**		*	ns	ns	ns
Diaphanasoma	H			ns		ns	†	***				
	T			ns		**	ns	ns				
	H x T			ns		ns	**	ns				
Ceriodaphnia	H				ns	ns			ns			ns
	T				ns	†			ns			ns
	H x T				ns	ns			ns			**
Moina	H	*	ns					ns				
	T	ns	***					†				
	H x T	†	†					ns				
Bosmina	H		ns			ns			ns		ns	
	T		ns			**			ns		**	
	H x T		**			ns			ns		ns	
Chydorus	H		ns	ns			ns		ns			
	T		ns	**			ns		ns			
	H x T		**	†			ns		ns			
Cln.copepod	H				ns	ns	†	ns			ns	
	T				ns	ns	ns	ns			ns	
	H x T				ns	ns	ns	ns			ns	
Anureopsis	H	ns										**
	T	ns										ns
	H x T	ns										**
Brachionus	H		*	**								**
	T		***	ns								ns
	H x T		ns	ns								ns
Hexarthra	H	ns	*									
	T	ns	ns									
	H x T	ns	ns									
Filinia	H			*				ns				
	T			ns				**				
	H x T			ns				ns				
Asplanchna	H								ns			
	T								ns			
	H x T								**			

3.3.4. Assemblage of potential predators

In the lakes no obligate piscivorous fish appeared except in Lakes Hamam, Küçük Akgöl and Taşkısığı and all other lakes were dominated by cyprinids (Table 3.4). Among the fish species planktivorous *Pseudorasbora parva* was observed remarkable high whereas, *Scardinius erythrophthalmus, Abramis brama, Leuciscus cephalus and Alburnoides* sp. was also caught very high density in lakes. The ratio of plant:open water fish increase significantly in lakes which were ordered according to latitudinal gradient ($R_{sqr}= 0.64$, $p<0.05$) and planktivorous fish were more abundant inside the plant beds than in open water (Fig. 3.6) whereas the <10cm sized fish were also found at low Secchi depth ($R_{sqr}=0.66$, $p<0.01$). Moreover the plantivorous fish density was negatively related with the zooplankton size diversity ($R_{sqr}= 0.43$, $p<0.05$) (Fig. 3.7) which was reflect to the predation pressure on zooplankton.

The predatory midge *Chaoborus* was detected in Lakes Emre, Karagöl, Küçük Akgöl and Saklı at night, but not during the day at open water sites. Moreover predatory *Leptadora* was detected only in Lake Taşkısığı during night.

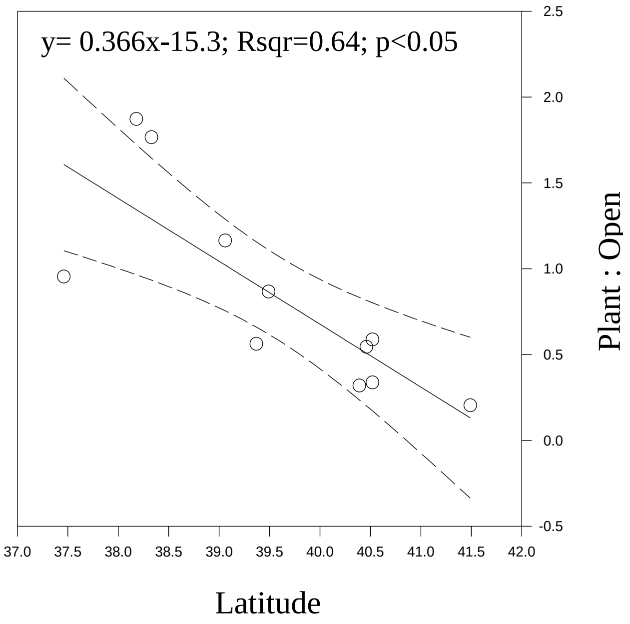

Figure 3.6. Relationship between plant:open water plantivorous fish ratio and latitude where the sampled lakes ordered.

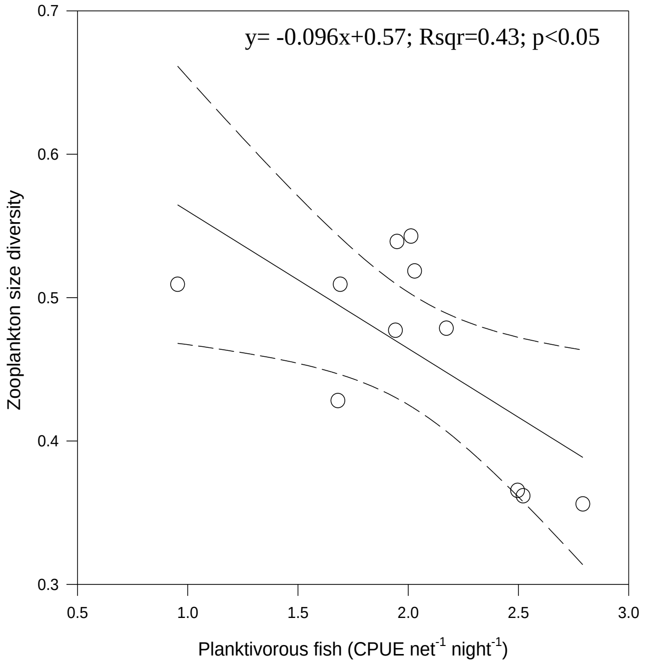

Figure 3.7. Relationship between zooplankton size diversity and planktivorous fish abundance.

Table 3.4. Mean fish density (ind. net^{-1}) with standart error (SE) of fish species captured in each lake. Abundance of fish species per net per night were given in the bracket.

	Hamam	**Küçük Akgöl**	**Taşkısığı**	**Yeniçağa**	**GölcükB**	**Eymir**	**Mogan**	**Emre**	**Karagöl**	**GölcükÖ**	**Saklı**
FISH SPECIES											
Abramis brama		4.0±1.2 (70)	2.0±1.2 (25)								
Alburnus sp.	1.0±1.0 (9)	3.0±1.5 (55)		1.0±0.0 (0.4)		1.0±0.0 (1.5)	3.2±1.8 (60.5)				
Alburnoides sp.								10±0.8 (100)			
Atherina boyeri	11±1.0 (32)		4.2±4.6 (16)								1.0±0.0 (3)
Cyprinus carpio				1.0±2.3 (6.9)		1.0±0.0 (13.5)		1.0±0.3 (2)			
Carassius carassius	1.0±0.0 (3)							1.0±0.0 (1)	1.0±0.0 (4)	1±3.5 (4)	1.0±0.0 (6)
Carassius auratus								1.0±0.0 (2)			
Cobitis taenia							1.0±0.0 (0.3)	1.0±0.0 (1)			
Gobio gobio				1.0±0.0 (0.3)				3.0±0.7 (2)			
Leuciscus cephalus				10±0.1 (81)	2.0±0.3 (43)						
Perca fluviatilis		1.0±2.2 (24)	4.0±0.5 (4)								
Pseudorasbora parva						3.0±0.8 (24.5)	14±0.9 (269)				
Petroleuciscus smyrnae									5.0±0.5(84)		
Rhodeus sp.	1.0±0.0 (1)										
Rutilus rutilus										12±1.1 (46)	
Scardinius erythrophthalmus	3.0±0.5 (43)	3.0±1.4 (61)	3.0±0.7 (75)								
Stizostedion lucioperca	1.0±0.0 (4)										
Tinca tinca				2±1.0 (30)	1.0±0.0 (5)	1.0±1.6 (10)	1.0±0.0 (2)				
Y-O-Y		45±1.0(432)	66±0.7(198)	11±(102)		26±1.4 (53.5)					

3.4. Discussion

We found major changes in the taxon composition and size structure of zooplankton in the studied shallow lakes coinciding with a change in fish density and fish habitat preference. Size diversity was also negatively related to fish density, with narrower size distributions and dominance of smaller sizes when fish predation pressure increased. Moreover, the geometric mean of the zooplankton did vary neither temporal (day-night) nor spatial (submerged plant-open water) which tends to homogenise the size structure in lakes through fish predation. Our results agreed with a previous study (Brucet et al. 2010) which showed a predominance of small sized taxa in Mediterranean lakes as a result of high predation pressure. However in temperate lakes, bimodal zooplankton size distribution, with the second peak reflecting the occurrence of large sizes.

Habitat uses of fish display differences between colder, high density within free-floating plant, and warmer, more associated with submerged plant, lakes (Jeppesen et al., 2010a). Increased fish density in or near the plant induced vertical migration of most zooplankton taxa, including rotifers. In our results, under the predation risk, zooplankton abundance was found remarkably high during night both in open habitat and submerged plants. Aggregation of zooplankton near the lake bottom during the day and prevalence of DVM are in agreement with previous laboratory habitat choice experiments (Tavşanoğlu et al., 2012) in which *Daphnia magna* did not use submerged plant as a refuge when facing a predation risk from fish, but preferred to stay near the sediment. Such as in Lake GölcükB, where the spatial distribution of fish was homogenous thus causing a higher predation risk in both habitats, zooplankton underwent diel vertical migration. While free-swimming cladocerans, *Ceriodaphnia*, despite low abundance, were performing reverse horizontal migration in Lake Yeniçağa, may probably as a result of spatial distribution of fish which was highly associated with plant and lack of pelagic predator.

Moreover, the effect of the macroinvertebrate predator *Chaborus* is likely to trigger reverse vertical migration not only for the large sized but also for the rotifers.

Although no quantitative data is available on macroinvertebrate predators in the present study, except our absent/present data of *Chaoborus*, macroinvertebrate predators were recorded in other Anatolian lakes (Toksöz &Ustaoğlu, 2005; Taşdemir et al., 2008; Saraoğlu, 2012).

Moreover, several studies indicate reverse migration of zooplankton in response to *Chaborus* predation (Gliwicz, 2000; Young &Riessen, 2005; Lagergren et al., 2008).

Our results support the predator avoidance hypothesis; larger taxa such as *Daphnia* in Lake Eymir displayed vertical migration to avoid fish predation since the size classes of *Daphnia* larger than 1.4 mm preferred to stay at the bottom during the day. Despite there was no migration detected in Lake Yeniçağa using whole abundance data without considering sizes, the size classes of *Daphnia* larger than 1 mm exhibited vertical migration whilst the ones smaller than 1 mm continued to survive during day without searching a refuge. Other experimental studies have also showed that approximately 0.9 mm sized *Daphnia* respond to predator by migrating bottom during day (Hansson and Hylander, 2009). However, in Lake Emre smaller taxa such as *Ceriodaphnia, Chydorus* and also worse swimmer rotifers, displayed reverse migration probably to avoid *Chaborus* predation. Furthermore, despite *Ceriodaphnia* underwent vertical migration in Lake Saklı, under the predation risk, approximately larger than 0.5 mm sized individuals reside at the bottom where the size classes below that did not displaced temporally. Size dependent feeding may probably favour larger species and attain size-refugia (Woodward & Hildrew, 2002). Furthermore, larger individuals preferred to displace their diel aggregation within the habitat depending on the visual/tactile predator. However, smaller individuals were not vulnerable as larger ones to the predation (Hansson and Hylander, 2009).

In accordance with the low water clarity Lake Karagöl, *Daphnia* was present and no significant migration pattern could be discerned, which may reflect a reduced prey encounter rate of visual predators in this turbid lake (Nurminen et al., 2008a); turbidity may also serve as a refuge for zooplankton, allowing survival of large-sized *Daphnia* (Merhoff et al., 2007a*).*

Rotifers in which the size range was very narrow, on the other hand, displayed both vertical and reverse vertical migration pattern. Crustacean zooplankton and juvenile fish were feed on rotifers thus larger individuals were preferred to display their spatial aggregation. In lakes where we observed migration was highly dominated by the juvenile fish or exist predatory midge. Thus the coexistence of large predators is probably due to morphological or behavioural traits to defend them against predator. However, this result should be interpreted in caution since there were shortcomings on the morphological traits of rotifers in the present study. Our results concurred with the earlier findings on the migration pattern of zooplankton for warm lakes (Meerhoff, 2006, 2007a; Castro et al., 2007); however these studies did not assess the migration by using size classes.

In the present study, zooplankton geometric mean was not low despite fish density in saline Lakes Eymir and Mogan in contrast to previous studies (e.g. Jeppesen et al., 1994; 1997, Jensen et al., 2010; Brucet et al., 2009; 2012). However, the zooplankton taxa were consisting of large-bodied grazer, *Daphnia magna*, a freshwater organism tolerates salinities up to 7.8 g L^{-1} (Schuytema et al., 1997), and calanoids. Although Jensen et al. (2010) suggested that fish density, particularly that of small planktivorous fish, within the plants influences diel vertical migration, which was the most frequent pattern observed along the whole salinity gradient (from almost freshwater to oligohaline). Since salinity gradient was obviously very narrow in the present study, there is also need for clarifying the size structure and migration patterns in saline lakes for this region.

We conclude that predators most likely exert an important influence on zooplankton size structure and diel movement for a number of Anatolian shallow lakes. Furthermore, the use of submerged plants as a refuge by zooplankton may be weak and water transparency may therefore decrease due to reduced grazing on phytoplankton. This study suggests that a size-based approach is a very useful tool to elucidate the predator-prey interactions in shallow lakes.

CHAPTER 4

SEDIMENTS, NOT PLANTS, OFFER THE PREFERRED REFUGE FOR *DAPHNIA* AGAINST FISH PREDATION IN MEDITERRANEAN SHALLOW LAKES: AN EXPERIMENTAL DEMONSTRATION[1]

4.1. Introduction

Zooplankton play an important role in freshwater ecosystems since they act as a key link in the food chain via their consumption on phytoplankton and also constitute the typical prey of many fish (Lauridsen et al., 1999; Gyllström et al., 2005; Jeppesen et al., 2011). Fish predation is often the key factor shaping the composition and body size distribution of zooplankton communities in lakes (Gliwicz, 1994). Chemical signals, either kairomonesreleased by the predators or ‘alarm signals’ released by injured conspecifics (Pijanowska, 1997), warn the prey against the presence of potential predators (Brönmark & Hansson, 2000; Mikulski & Pijanowska, 2010) and may significantly affect predator–prey interactions (Lass & Spaak, 2003). Diel vertical migration (DVM) has been shown to be an important anti-predator defence mechanism in deep stratified lakes (Gliwicz, 1986; Lampert, 1989). In contrast, in shallow lakes, large-bodied zooplankton (typically cladocerans) often aggregate within submerged plant stands during daytime and move to the open water to graze on phytoplankton at night when the risk of predation abates (Timms & Moss, 1984; Lauridsen & Lodge, 1996). This well-known behaviour is termed ‘diel horizontal migration’ (DHM) and has mostly been observed in north temperate shallow lakes (Burks et al.,2002). An increasing amount of field data as well as laboratory experiments suggest that the use of spatial refugia and the type of migration behaviour vary according to the structure, biomass and feeding mode of the fish community(Meerhoff et al., 2007a; Jensen et al., 2010), which seem to alter according to climate regime (Teixeira-de Mello et al., 2009).

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[1] This chapter was published in Freshwater Biology (2012): 57, 795–802

The predation pressure by fish appears to be higher in warm climates (Gyllström et al., 2005; Meerhoff et al., 2007b; Jeppesen et al., 2010).

Thus, in Mediterranean shallow lakes, investigations have shown dominance by omnivorous fish (Blanco et al., 2003) that exert a strong predation pressure on the zooplankton (García-Berthou, 1999), as indicated by dominance of small-sized zooplankton (Romo et al., 2004; Beklioglu et al., 2007; Brucet et al., 2010). A less studied subject is the behavioural responses of Mediterranean lake zooplankton to the risk of predation. In subtropical lakes, findings indicate that submerged plants do not act as a zooplankton refuge (Meerhoff et al., 2006, 2007a), the most likely explanation being the high abundance of fish, particularly small-sized species, within the vegetation (Mazzeo et al., 2003; Teixeira- de Mello et al., 2009), and DVM seems to be the most common migration pattern (Meerhoff et al., 2007a,b). However, no experimental evidence exists documenting DVM as a behavioural adaptation in warm shallow lakes. Current knowledge is poor regarding predator avoidance strategies of daphniids in Mediterranean shallow lakes (Castro et al., 2007; Jensen et al., 2010), where potentially both DHM and DVM can occur since the fish communities present share characteristics with both temperate (e.g. species composition and spatial distribution patterns) and warm (e.g. predominance of small size classes) climates (Jeppesen et al., 2010; Beklioglu, M, in prep.). The aim of our study was to investigate the habitat selection of large-bodied *Daphnia magna* (Straus), collected from a Mediterranean shallow lake, by exposing them to predation cues in a 'habitat choice' laboratory experimental set-up, permitting both horizontal and vertical movements. The experimental design allowed us to elucidate the effectiveness of plants (the submerged macrophyte Canadian pondweed, *Elodea canadensis* Michaux) and sediments (black inert sand) as a refuge by observing the response of *D. magna* to predation cues (derived from fish kairomones and crushed conspecifics).

Based on the previous findings in warm lakes (e.g. Mediterranean and subtropical lakes), we hypothesized that the *Daphnia* would not hide among the submerged plants when exposed to a risk of predation, but rather find refuge near or in the sediment.

4.2. Material and Methods

4.2.1.Experimental set-up

To test the response of Daphnia to chemical cues at a horizontal and vertical scale, experiments were run in a special set-up modified from Meerhoff et al. (2006), allowing horizontal and vertical zooplankton migrations (Fig. 4.1).

Figure 4.1. Experimental set-up designed to test the horizontal and/or vertical movement of *Daphnia*. The disc inside each tank could be removed in accordance with the particular objective of the experiment. Both discs could be moved up and down as shown to the right.

The experimental unit consisted of two transparent cylindrical tanks (diameter, 20 cm; height, 100 cm) connected to each other by a plexiglass tube (diameter, 5 cm; length, 100 cm). Each tank could be closed by a cylindrical disc to create 23-cm- and 46-cm-deep sections (Fig. 4.1). The water flow between the tanks ensured the generation of a gradient of the chemical cues. Prior to the experiments, we tested in triplicate the diffusion pattern of dye (methyl blue), which reached the other tank in ca.50 min (Fig 4.2).

Figure 4.2. Diffusion of dye (methyl blue) in the experimental set-up.

The experiments were performed in a dark room with halogen lamps (12 V) illuminating the tanks from the top through frosted glass at 30-cm distance. The experimental set-up was surrounded by styrofoam walls at 30-cm distance to prevent external light interference. *Daphnia magna* (Straus) were collected from Lake Eymir, Turkey (39 57 ºN, 32 53 ºE), and pre-incubated for 2 weeks in a controlled climate room (22 ± 1 ºC) with a photoperiod of 16 : 8 h light : dark cycles. The individuals used did not derive from a single clone. During the pre-incubation, the *D. magna* were fed regularly with dried yeast.The cultures were acclimated to the de-chlorinated tab water in the laboratory. *Elodea canadensis* was used in the plant experiments. *Elodea canadensis* was first introduced to Europe in the 1840s and has been observed in Turkey since the 1980s (Kesici et al., 2009).

We obtained the plants from a local aquarium dealer and placed eight shoots of Elodea inside the tanks with a percentage volume inhabited (PVI) by plants of ca.80% (PVI sensu Canfield et al., 1984, calculated by measuring submerged plant cover, plant height and water depth). We also used plastic plants, mimicking *E. canadensis* and with the same %PVI, to determine whether any plant effects on the behaviour of *D. magna* were induced mechanically or chemically. For fish cue production, we used 4.0–6.0-cm individuals of topmouth gudgeon [*Pseudorasbora parva* (Temminck & Schlegel)], an abundant planktivore in Lake Eymir (Beklioğlu et al., unpubl. data). Plants and fish were kept in the controlled climate room under the same light cycle and temperature conditions as described above.

For the sediment experiments, we used artificial black aquarium sand (sized 1–3 mm, approximately 2-cm layer) to prevent the presence of potential previous cues.

4.2.2. Preparation of treatments

We used dechlorinated tap water without chemical signals as a control medium (C). For the production of predation cues, three *P. parva* were incubated overnight (about 18 h) in 10 L of dechlorinated tap water. *Pseudorasbora parva* was fed commercial fish food before the experiment. We collected 2 L of water from this incubation medium and added a homogenate of 100 crushed *Daphnia* (50 ind. L^{-1}) to produce ‘alarm signals’ (sensu Pijanowska, 1997). The cued water was filtered through a 0.45-mm pore cellulose nitrate membrane filter (Millipore Corporation, Bedford, MA, USA) before the experiments. We used a combination of kairomones and alarm signals to obtain a strong predation cue. The experimental unit was filled with dechlorinated tap water (17 L) before addition of the respective treatments. Once the cue had been introduced, we waited 30 min, based on the experimental results with dye described previously, to allow the build-up of a chemical gradient. Then, we gently added ten *D. magna* (ca. 2 mm in size) to the centre of the connecting tube and recorded their position every 15 min.

The *Daphnia* found within the treated tank were ‘attracted’ to the cue, while the *Daphnia* in the untreated tank were ‘repelled’ from the cue. When the daphniids remained in the horizontal connecting tube in the middle, they were either ‘attracted to’ or ‘repelled from’ the cue depending on the half in which they occurred, the half furthest from the treated tank being the ‘repellence’ zone and the half nearest the treated tank the ‘attraction’ zone. Daphniid movements were recorded 15, 30, 45, 60, 75 and 90 min after a 15-min acclimation period.

The height of each cylindrical tank was adjusted via an internal disc to the same level (23 cm) for the simple ‘horizontal migration’ experiments 1–6 (Table 4.1; Fig 4.3.). In experiment 7 (Table 4.1), the height of one tank was increased to 46 cm, while the other remained at 23 cm.

Through this height adjustment, we created a shallow littoral and a deeper pelagic where the artificial sediment was added to the bottom. Otherwise, we followed the procedures described below. Single treatments (repellence–attraction experiments) included *E. canadensis* with 80% PVI, artificial plants mimicking Elodea with the same % PVI, sediments and predation cues, all in one tank, while the other tank contained only dechlorinated water.

Double treatments (choice experiments), in which the treatments differed by side of the experiment unit, included *E. canadensis* versus predation cues (testing DHM), sediments versus predation cues (testing DVM) and sediments (plus predation cues) versus plants (plus predation cues) (testing DHM or DVM) (Table 4.1; Fig 4.4.). We repeated each experiment five times for replication, and each time we changed treatment side to avoid any bias on daphniid movements. Moreover, we always used new individuals and rinsed the experimental unit thoroughly with distilled water before each new run.

Table 4.1. Summary of study experiments indicating treatments and hypotheses tested and the methodology employed.

No. Short name	**Hypothesis**	**Method**
1 *E. canadensis*	*Daphnia* avoid plants	plants covering one tank
2 Artificial plant	Plant avoidance is mechanically-induced	artificial plants covering one tank
3 Predation cues	*Daphnia* avoid predators	2L predation cues in one tank
4 Sediments	*Daphnia* avoid sediments	artificial sediment in one tank
5 Refuge: plant	*Daphnia* seek refuge in the plants	combination exp 1+3
6 Refuge: sediment	*Daphnia* seek refuge in the sediment	combination exp 4+3
7 Refuge preference	*Daphnia* seek refuge in the sediment	combination exp 1+4+3 (both side with predation cues)

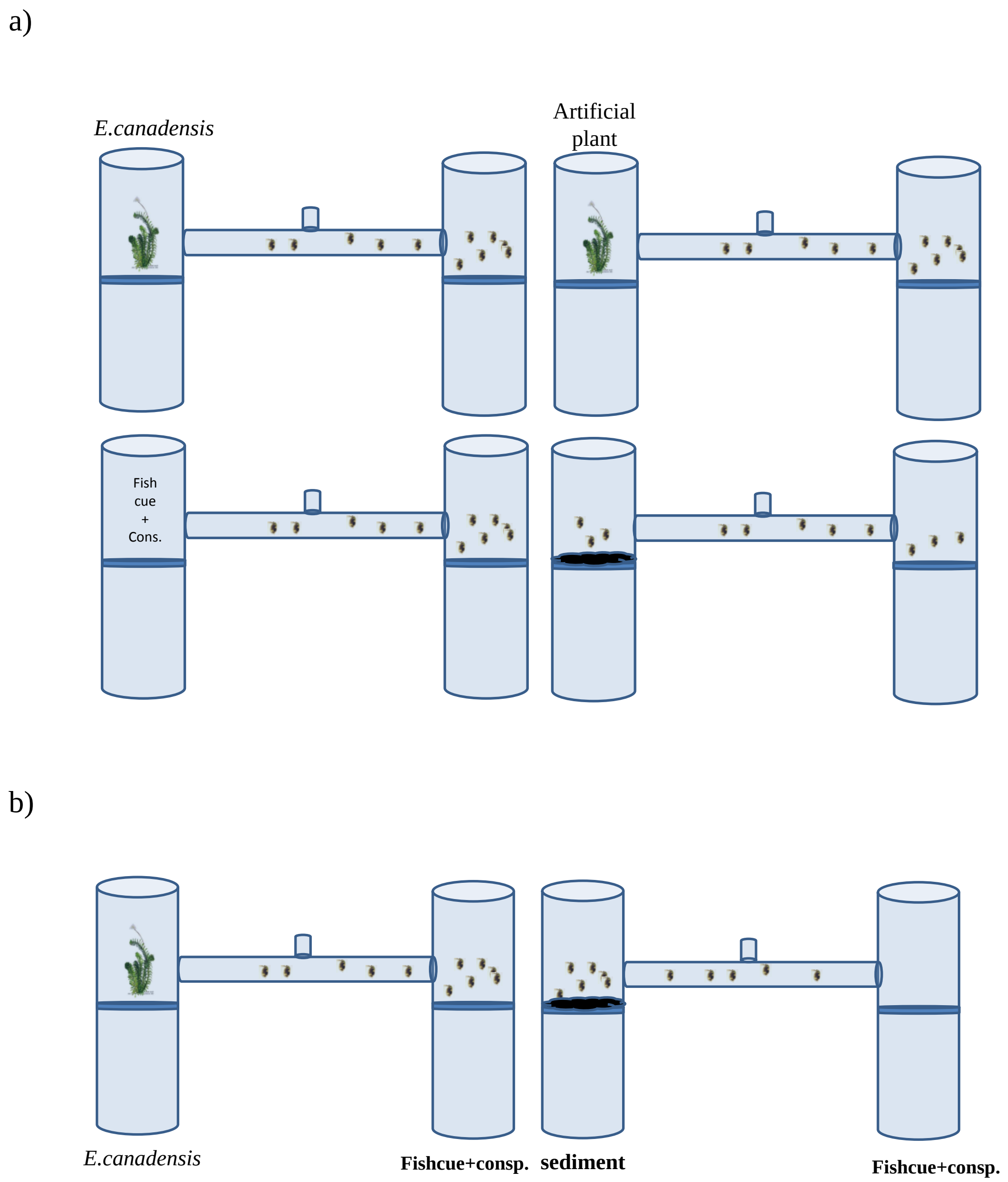

Figure 4.3. Single treatments: a) Cue vs. Control, b) Repellence-attraction tests.

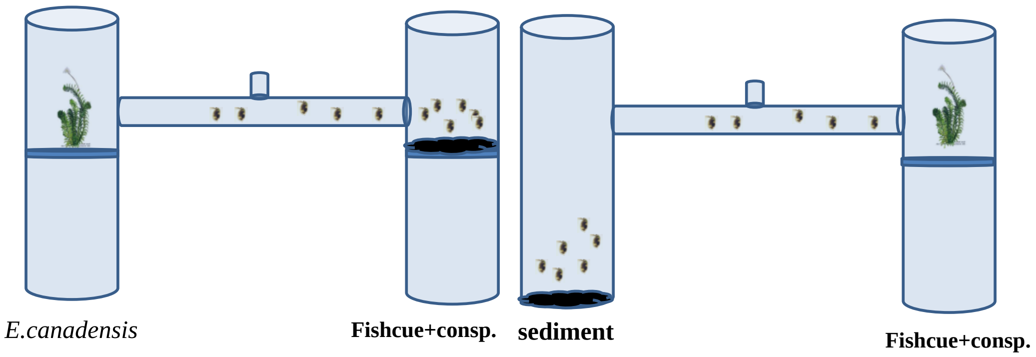

Figure 4.4. Double treatments (choice experiments: Plant vs. Sediment).

4.2.3. Statistical analyses

After checking for the lack of temporal trends in the behaviour of daphniids by visual inspection, we compared the responses of *D. magna* to each treatment using two-way repeated measures of ANOVA (RM-ANOVA), with treatment as main factor and time as the repeated measure. We conducted pairwise comparisons of the number of daphniids in the treatment versus control side of the unit (or double treatment) at specific times (15 min of the test period) using Student's t-tests. Owing to the multiple pairwise comparisons and the potentially enhanced risk of increasing type I errors (false positives), we used $P < 0.01$ as significant level and show the true P-values in the pairwise comparisons. For these analyses, we used the SAS software (SAS Institute Inc, Cary, NC, U.S.A.). We checked the normality of the data using the Shapiro–Wilk test and, if required, applied transformation (log10 (x+1) log10) prior to the statistical analyses (Sokal & Rohlf, 1997). When any requirement of parametric analysis was not met, nonparametric Mann–Whitney U-test was applied. These analyses were performed using the R statistical package (R Development Core Team, 2009).

4.3. Results

4.3.1. Daphnia response experiments

Daphnia responses to single cues *Daphnia magna* was repelled by both the real (RM-ANOVA $F_{1,8}$ = 18.69, P = 0.0025) and the artificial plants (RM-ANOVA $F_{1,8}$ = 43.58, P = 0.0002). After 15-min exposure to the cues, 80 ± 3% (SE) and 67 ± 7% (SE) of the daphniids moved away from the artificial plants (t = 9.48, d.f. = 8, P < 0.001) and real plants (t = 3.52, df = 8, P < 0.001), respectively (Fig. 4.5). Throughout the experiments, the response of *D. magna* was similar for real and artificial plants. Predation cues (crushed conspecifics plus fish cues) also repelled D. magna (RM-ANOVA $F_{1,8}$ = 16.59, P = 0.0036). After 15 min, 56 ± 8% (SE) of the *D. magna* were found in the opposite side of the treatment tank (Fig. 4.5). In contrast, when exposed to sediments only and in the absence of predator cues, the daphniids were evenly distributed within the experimental unit, with no statistically significant difference between sediments and control sides (RM-ANOVA $F_{1,8}$ = 0.39, P = 0.54) (Fig. 4.5).

4.3.2. Choice experiments: double cues

4.3.2.1. Plants as a refuge for Daphnia

Daphniids did not take refuge among the submerged plants when exposed simultaneously to submerged plants and predation cues (in opposite sides of the experimental unit) (RM-ANOVA $F_{1,8}$ = 31.62, P = 0.0005) (Fig. 4.6). After 15 min, 73 ± 12% (SE) of the daphniids had moved away from the plants and only 10% remained inside the plant-holding tank.

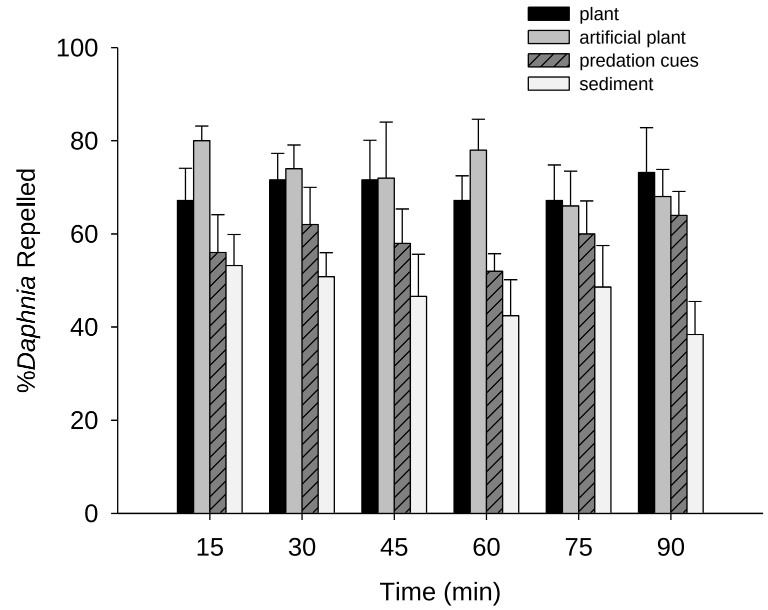

Figure 4.5. Effect of plants (real and artificial), predation cues and sediments on the horizontal movement of *Daphnia magna*. All experiments were conducted separately. Data represent the percentage of *D. magna* moving towards the control tank (i.e. the percentage repelled by the treatments) (mean ± 1 SE).

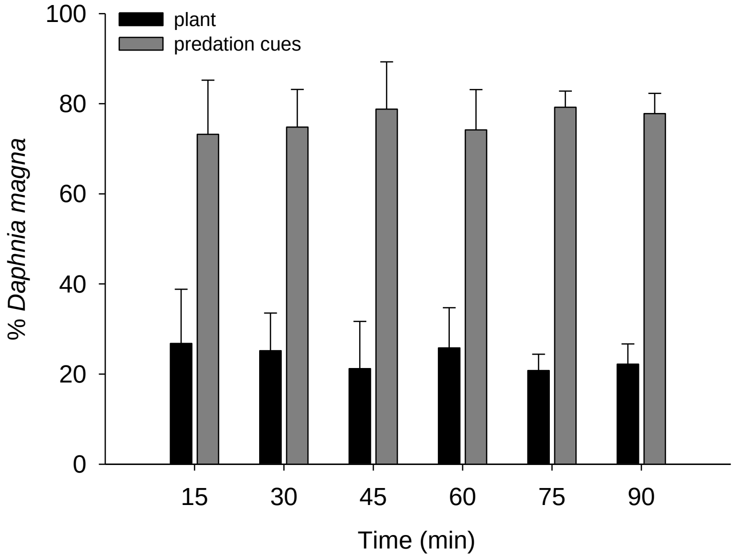

Figure 4.6. Response of *D. magna* exposed simultaneously to predation cues and submerged Elodea canadensis in opposite sides of the experimental unit. Data represent the percentages of *D. magna* in the predation cue and plant sides of the unit (mean ± 1 SE). If daphniids preferred plants over predation cues (i.e. the ‘refuge effect’), the % in the plant side would be >50%.

4.3.2.2. Sediments as a refuge for Daphnia

Daphnia magna moved towards the sediment-containing tank when facing predation cues in the tank without sediment (RM-ANOVA $F_{1,8}$ = 13.74, P = 0.006) (Fig. 4.7.). After 15 min, 80 ± 5%(SE) of the daphniids had swum away from the tank with predation cues to the sediment tank where they remained (15 min, t =)5.47, d.f. = 8, P = 0.005). With time, the refuge effect of the sediments persisted, but was abated. Although 62 ± 6% (SE) of the daphniids still occurred at the sediment side after 45 min, the differences were not statistically significant.

4.3.3. Choice between sediments and plants as refuge (DVM versus DHM)

When one side of the experimental unit contained plants and the other side sediments, both with the addition of predation cues, the response of daphniids was clear: they immediately moved away from the plant side towards the sediment side (RM-ANOVA $F_{1,8}$ = 84.38, P < 0.0001) (Fig. 4.8.). After 15 min, 68 ± 6% (SE) of the daphniids remained in the sediment tank, and only 8 ± 5% (SE) had moved to the plant tank. The distribution pattern remained the same throughout the experiment. In addition, we increased the height of one tank so as to mimic a 'deeper pelagic' zone with sediments and a 'shallow littoral' zone with plants in the opposite sides of the experimental set-up. In this experiment, the daphniids qualitatively displayed the same response as in the 'shallow' experiment, that is, after 15 min, 68 ± 9.7% (SE) % (t = 4.36, d.f. = 8, P = 0.002) had moved towards the sediment tank and away from the plants (RM-ANOVA $F_{1,8}$ = 9.08, P = 0.016) (Fig. 4.8.). In the sediment treatment, daphniids were mostly found near the bottom (P = 0.002, by Mann–Whitney rank-sum test); however, their use of the sediment decreased as the experiment went along, and at the end, the use of the plant and sediment tanks was similar (P > 0.05).

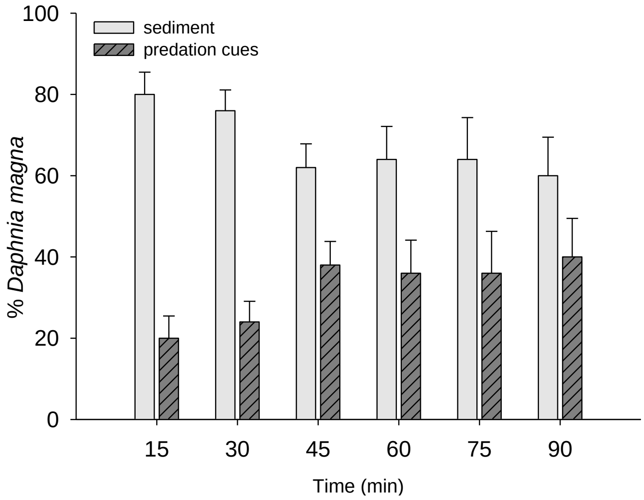

Figure 4.7. Response of *D. magna* exposed simultaneously to predation cues and sediments in opposite sides of the experimental unit. Data represent the percentages of *D. magna* in the predation cue and sediments sides of the unit (mean ± 1 SE).

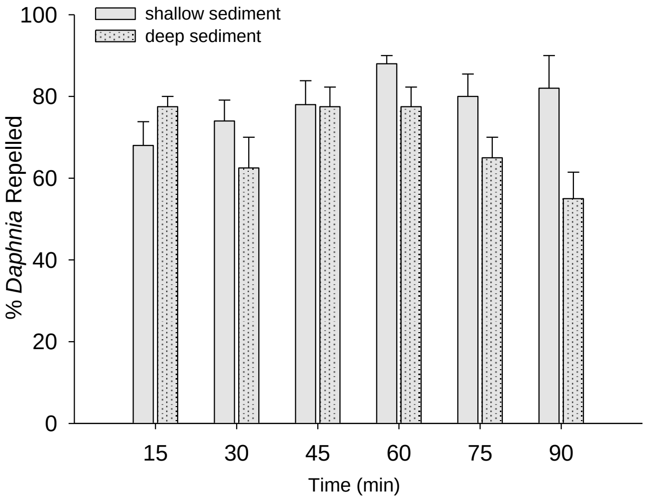

Figure 4.8. Response of *D. magna* exposed simultaneously to plants and sediments in opposite sides of the experimental unit, and with predation cues homogeneously distributed. Data represent the percentages of *D. magna* moving towards the sediment sides (repelled from plant side). In the shallow sediment experiment, the height of two experimental tanks was identical (23 cm), and in the deep sediment experiment, the height of one tank was increased to 46 cm, while the other remained at 23 cm. These two experiments were conducted separately.

4.4. Discussion

When facing *E. canadensis* alone, the *Daphnia* behaved as we could expect (Pennak, 1966, 1973). The aversion to both real and artificial plants indicates that the repellence is, at least partly, mechanically induced, as also found by Meerhoff et al. (2006). However, in contrast to studies from north temperate lakes (summarised by Burks et al., 2002), we found that *Daphnia* avoided the plants when exposed to predation cues, indicating that in Mediterranean lakes the behaviour triggered by the plants is more similar to that observed in subtropical shallow lakes (Meerhoff et al., 2006, 2007b). Exposed to only sediments and in the absence of predator cues, the daphniids were evenly distributed among areas with and without sediment. Consistent with our hypothesis, *D. magna* moved towards the sediments only when predation cues were added. However, when offered two potential refuge habitats against predation cues, *Daphnia* moved to the sediment and avoided the submerged macrophytes. This is the first experiment of its kind offering at the same time macrophytes (horizontal movement) and sediments (vertical movement) as refuge choices for Daphnia. Our experimental results concur with those from field studies in subtropical and other Mediterranean lakes where vertical movement of cladocerans has been shown to be the most frequent migration pattern for all habitats (Castro et al., 2007; Meerhoff et al., 2007a; Gonzáles Sagrario & Balseiro, 2010). Our results also concur with field experiments with artificial plants conducted in 16 Turkish shallow lakes, where zooplankton mostly appeared near the bottom during the daytime when the fish predation pressure expectedly was high (Tavşanoğlu et al., in prep.). The same holds true for Lake Eymir, the collection site for the daphniids used in the experiments, where we found a higher cladoceran abundance in the epilimnion of both the pelagic and littoral zones during night than during day (significant effect of ‘time’, $P < 0.05$, but no significant interaction), indicating that *D. magna* undertook DVM and that DHM was not important (Tavşanoğlu et al., in prep.).

Regular DVM is, however, less likely in lakes with a predominance of benthic predators such as the phantom midge *Chaoborus*. In such situations, reverse DVM may occur as seen in some Turkish shallow lakes (Tavşanoğlu et al., in prep.) and some deep lakes (Armengol & Miracle, 2000; Lagergren et al., 2008; Wojtal-Frankiewicz et al., 2010).

DVM therefore seems to be the most common antipredator avoidance behaviour in Mediterranean shallow lakes under the risk of high predation by fish. Our experiments and existing field evidence indicate that the behaviour of Mediterranean zooplankton concurs with that of subtropical rather than temperate lakes. This is despite the intermediate characteristics of the fish communities, with frequent dominance of small sizes (and a consequent high predation pressure on the zooplankton) as in subtropical lakes (Meerhoff et al., 2007a,b; Teixeira-de Mello et al., 2009), but a more homogenous use of space (Beklioglu et al., in prep.) including the pelagic, as in temperate lakes (Teixeira-de Mello et al., 2009). In subtropical lakes, the fish are seemingly attracted to the plant beds, resulting in a high predation risk for zooplankton among plants. In the experiment where the height of one tank was increased (to mimic a ‘shallow littoral’ zone with plants and a ‘deeper pelagic’ zone with sediments only, respectively), the daphniids displayed the same response as in the shallower tank: they moved towards the sediments and away from the plants. Interestingly, however, they remained in the sediment area for longer in the shallow tank, perhaps because of awareness of a higher predation risk in shallow waters. However, the alarm signal weakens rapidly in batch cultures (e.g. Beklioglu & Jeppesen, 1999), and we cannot exclude the possibility that this weakening was reinforced by the larger water volume in the set-up with deeper sediment tanks (leading to a weaker treatment effect at the end of this experiment).Our results from the experimental manipulation of depth suggest that water level reduction because of either management or climate warming (and compensatory autonomous changes in irrigation, Jeppesen et al., 2009) may not lead to a profound change in the anti-predator behaviour of zooplankton.

However, as the risk of fish predation might intensify when the lakes become shallower (Jeppesen et al., 2003; Meerhoff et al., 2007b), the effectiveness of sediments as a refuge could be jeopardised. The relative effectiveness and impact on zooplankton survival of using sediment rather than macrophyte as a refuge remain to be elucidated. In the subtropics, zooplankton biomass (Havens et al., 2009) and *Daphnia* mean body size (Iglesias et al., 2011) are frequently restricted by fish predation. The typical zooplankton structure in subtropical (Meerhoff et al., 2007a; Kruk et al., 2009) and Mediterranean (Beklioglu et al., 2007; Brucet et al., 2010) shallow lakes seems to support the theory that DVM does not suffice to counteract the high predation pressure (that adds to other environmental stressors such as higher temperature and sometimes also salinity) in these systems. We conclude that *Daphnia* in Mediterranean shallow lakes prefer to find refuge near, or possibly even in, the sediments and not among plants when facing a risk of predation. This behaviour is not likely to change if the lakes become shallower because of climate warming or increased water extraction, although the efficiency of the sediment refuge may not suffice to allow the build-up of large daphniid populations.

CHAPTER 5

ZOOPLANKTON COMMUNITY RESPONSES TO DROUGHT INDUCED SALINITY AND EUTROPHICATION IN TWO INTERCONNECTED TURKISH SHALLOW LAKES

5.1. Introduction

The wet winters and hot dry summers are the characteristics of semi-arid Mediterranean climate thus lakes located in Mediterranean climate subjected to large water level variation as a result of rainfall seasonality and discharge/re-charge of groundwater (Naselli-Flores, 2005; Alvarez-Cobelas et al., 2005; Beklioğlu et al., 2007). As a result of lake-aquifer model, small but long term changes in precipitation and temperature resulting significant decreases in lake levels (Yağbasan and Yazıcıgil, 2012). Water level fluctuation has a vital effect on the aquatic system such as underwater light availability, nutrient level, growth dynamics, primary production, and community relationships (Wallsten & Forsgren, 1989; Blindow, 1992; Beklioğlu et al., 2001; Tan & Beklioğlu, 2006).

However, predictions of global climate change suggested that Mediterranean region will experience 20-23% lower precipitation and higher evaporation whereby lead to extreme drought (Williams, 2001; Giorgi, 2006). As a result of drought, internal processes may induce nutrient enrichment may and it became predominant and exacerbates eutrophication (Özen et al., 2010; Jeppesen et al. 2009; 2010b). Drought may also induce salinization of freshwaters (Beklioğlu & Tan, 2008; Beklioğlu et al. 2011).

Since global climate change affect the water level of lakes and trigger prolonged drought periods causing salinization in lakes. Although there are no clear-cut defined borderlines between fresh and brackish waters, 0.5‰ is considered as the lower limit of brackishness (Moss, 1994).

Salinity is an important factor influencing freshwater organisms (Baillieul et al., 1996) that negatively affects survival and life history of zooplankton (Hart et al. 1991; Hall & Burns, 2002; Grzesiuk & Mikulski, 2006; Sarma & Nandini, 2006). Brackish lakes there has been strong predation pressure on zooplankton by planktivorous fish which have several cohort per year (Jeppesen et al., 2007) and fish fry which may abundant during summer and also in autumn (Jeppesen, 1998). Furthermore, owing to the strong predation pressure trophic structure of the lakes changes along the salinity gradient shift from large sized cladocerans to small cladocerans, rotifers and calanoid copepods (Jeppesen et al., 2007; Brucet el al., 2009; Jensen et al., 2010) thereby weaken the top-down control on phytoplankton (Brucet et al., 2010). In addition, species richness of zooplankton was negatively related with salinity (William et al., 1990; Walsh et al., 2008; Jensen et al., 2010). Consequently, eutrophic brackish lakes display similar pattern with some eutrophic subtropical and Mediterranean freshwater lakes being frequently turbid and consisting of small bodied zooplankton owing to strong predation pressure (Gyllström et al, 2005; Meerhoff et al., 2007b; Beklioğlu et al., unpubl data). As a multiple stress factors interactions both salinity and fish interaction yields to an antagonistic impact on zooplankton (Hart et al. 1991; Hall & Burns, 2002; Grzesiuk & Mikulski, 2006; Sarma & Nandini, 2006; Bezirci et al., 2012).

Several researches indicated that warm lakes are more sensitive to eutrophication than temperate lakes (Moss et al., 2004; Jeppesen et al., 2007; 2009; Brucet et al., 2010). On the other hand, cold and warm shallow freshwater lakes and brackish lakes have different trophic interactions (Bachmann et al., 2002; Havens et al., 2007; Brucet et al., 2010; Meerhoff et al., 2012). Nutrient rich brackish lakes are turbid despite high density of submerged macrophyte (Jeppesen et al., 1994; Jeppesen et al., 1997). Meanwhile, in freshwater lakes macrophytes lead to improve water transparency via strong grazing of zooplankton that macrophytes serve as a refuge for zooplankton against fish predation (Burks et al., 2002; Lauridsen & Buenk, 1996; Lauridsen et al., 1998). However, Bachmann et al., (2002) indicated that in warm lakes there was no significant relation observed between macrophyte growth and water clarity. Furthermore, in warm lakes, the fish community consisted of small omnivorous specimens which may enhance the predation pressure on zooplankton (Meerhoff et al., 2007a,b; Teixeira-de Mello et al., 2009; Jeppesen et al. , 2010a) and may reduce clear water state (Meerhoff et al., 2007a,b).

Since higher temperature enhanced the reproduction, faster growth and reduced longevity of fish (Blanck and Lammouroux, 2007; Jeppesen et al., 2010a) resulting the decrease large sized zooplankton. Similar results were obtained from southern lakes of Turkey that experience higher biomass of small fish (Beklioğlu et al., unpubl data).

Removal of plankti-benthivorous fish termed as biomanipulation as a restoration measure has been widely and successfully used in temperate (Jeppesen et al., 1990a; Jeppesen et al., 1990b; Hansson et al., 1998). However, the success of fish removal has been obstacled with repetitive fish breeding and high small fish density in warm lakes (Jeppesen et al., 2005) with some exceptions of high altitude warm lakes (Beklioğlu et al., 2003; Beklioğlu & Tan, 2006). Furthermore, in Mediterranean region success of biomanipulation may considerably hindered drought induced eutrophication through water level fluctuation in semi-arid region (Beklioğlu & Tan, 2006).

The present study covers 15 years data from 1997 to 2011, which is the first extensive dataset from Turkey, belonging to two interconnected shallow Lakes Mogan and Eymir located in Central Anatolia. During the study period, there were drought and wet periods that strongly controlled the nutrient levels and salinity thus the food web interactions in the both of the lakes as well as a restoration of eutrophic downstream Lake Eymir through biomanipulation twice (Beklioğlu & Tan, 2008; Özen et al. 2010; Beklioğlu et al., 2011). Thus the main aim of this study was to investigate the long-term physical, chemical and fish data analyzed for determining the factors influencing the zooplankton community composition in the both lakes.

5.2. Material and Methods

5.2.1. Study Sites

Lake Mogan (surface area 5.4 km^2) and Lake Eymir (surface area 1.2 km^2) are interconnected together and located in Central Anatolia (39° 47' N 32° 47' E; 39° 57' N 32° 53' E respectively).

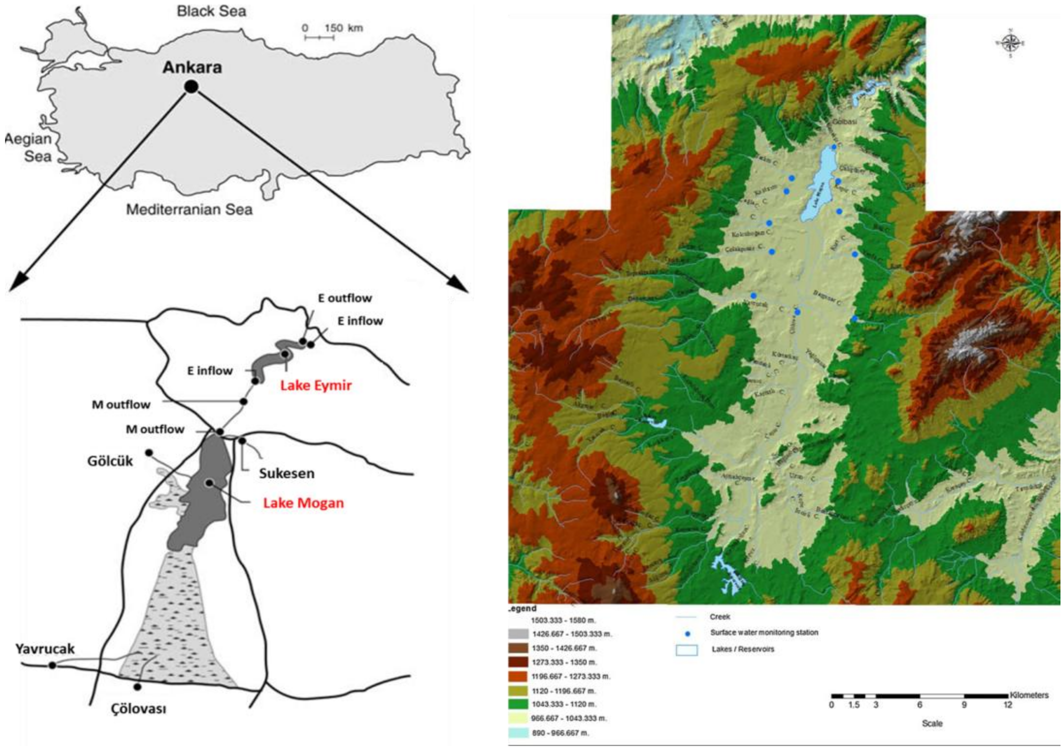

Figure 5.1. The location of study and the sampling sites. Relief map was taken from Yağbasan & Yazıcıgil (2012).

Lake Eymir is located as downstream of Lake Mogan. The catchment covers 985 km^2 and the location of lakes was northeast part of the catchment that the formation was tectonic depression and named as Gölbaşı formation. The lakes are relatively shallow (Z_{mean}=2.1m and 2.6-3.2m in Lakes Mogan and Eymir, respectively) alluvial dam lakes (Fig. 5.2.).

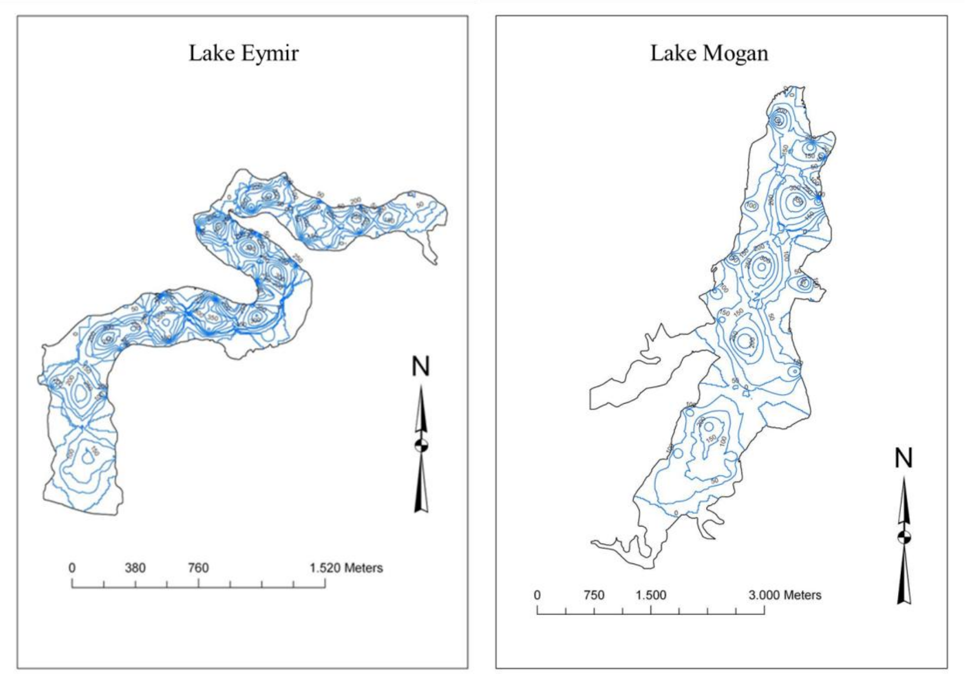

Figure 5.2. Batimetry map of Lakes Eymir and Mogan (drawn by Korhan Özkan using ArcView, unpublished data of METU, Limnology Laboratory)

Sukesen, Gölcük, Yavrucak and Çölovası brooks are the main inflows of Lake Mogan (Fig. 5.1.). Furthermore, the man made reservoirs (Dikilitaş and İkizce) are located upstream of Lake Mogan and have significant impacts on the water level (Yağbasan and Yazıcıgil, 2009).

The outflow of Lake Mogan runs through wetland called Gölbaşı Düzlüğü from which water feeds Lake Eymir through both surface and underground waters. Moreover, the other inflow of Lake Eymir is Kışlakçı brook and the lake waters flows out to the İmrahor Creek to the northeast. The surface inflows of Lake Eymir are mostly dry out in summer (Beklioğlu et al., 2003; Özen et al. 2010).

In Lake Mogan, there was no biomanipulation afford. Previous researches indicated that the lake was in clear water state with macrophyte domination (Burnak & Beklioğlu, 2000) and the ecological state of the lake is very sensitive to hydrological alteration namely water level fluctuation (Zhang et al., 2003a; Zhang et al., 2003b).

During low water level year’s in-lake TP and nitrate concentration was found high indicating internal loading. In addition annually 44-65% of the lake volume was loss as a result of evaporation (Özen et al., 2010) indicating the sensitivity to salinization. Moreover, data consisted of 1999 to 2008 displayed that groundwater level decreases remarkable (Fig. 5.3.).

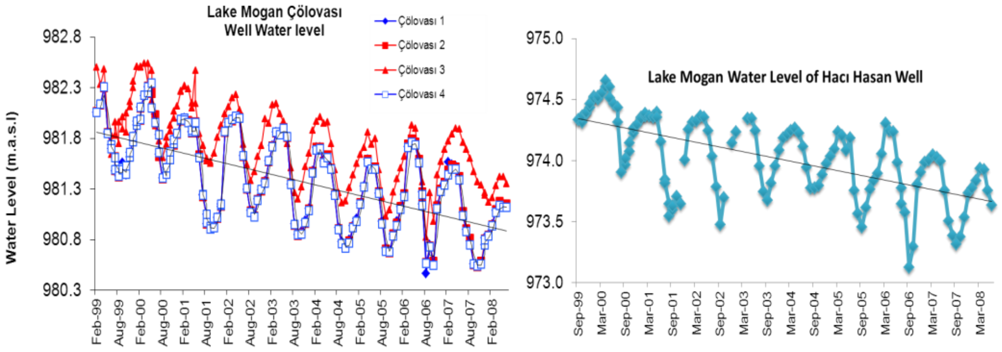

Figure 5.3. Changes in water level of the main well stations in Lake Mogan from 1999 to 2008 (EIE, 2009).

Low water level led to high vegetation cover in Lake Mogan (Beklioğlu et al., 2006). In addition, submerged plant (*Potemogeton pectinatus* L) development was not affected by the dense fish and waterfowl in spring (Sandsten et al., 2005). However submerged plant redeveloped may occur as low TP as 0.1 mg TP L^{-1} (Zhang et al., 2003b).

Fish community of lake included *Esox lucius*, Linnaeus 1758 (pike), *Tinca tinca*, Linnaeus 1758 (tench), *Cyprinus carpio*, Linnaeus 1758 (carp) (DSI, 1993; ÖÇKK, 2002, Manav & Yerli, 2008), *Siluris glanis*, Linnaeus 1758 (catfish) was also caught (Akbulut & Akbulut, 2002). Lately exotic species *Pseudorasbora parva* (Temminck & Schlegel, 1846) were recorded (Beklioğlu et al., unpubl data). Furthermore the contribution of pike was high in the 1990s and early 2000 then the fish stock became mostly consisting of tench and carp (DSİ, 1993).

Moreover the lake and surrounding wetlands were also hosting more than 160 different bird species (Özesmi, 1999) thus since 1990 Lake Mogan became 'Specially Protected Area' and has been designated as an Important Bird Area. Lake was close to the Ankara (Capital city) and mainly served as recreational purposes.

Lake Eymir served as a drinking water supply for Middle East Technical University which owned the lake since 1958, until 1990. Lake Eymir received raw sewage effluents over 25 years from 1970s until 1995 (Altınbilek et al., 1995; Beklioğlu et al., 2003) then sewage diversion was undertaken. Despite the diversion reduced the in-lake total phosphorus, water clarity was still low in 1997. During the period of 1998 to 1999, fifty percent of tench and carp were removed and pike angling was banned (Beklioğlu et al. 2003). First year after biomanipulation, the water clarity improved and macrophytes returned with a large coverage from 30%-80%.

However, the recovery started to deteriorate through prolonged drought that increased nutrients through internal mechanisms (Beklioglu & Tan, 2008; Özen et al. 2010). Consequently, the fish biomass increased again to the pre-biomanipulation level. Upon deterioration, second biomanipulation has been initiated since 2006 by tench and carp have still been removed.

Moreover, after 2006 exotic *Pseudorasbora parva* (Temminck & Schlegel, 1846) was recorded in Lake Eymir. *P. parva* was first recorded from lakes in Thrace region (Erk'akan, 1983) and reported several inland waters in Turkey (Şaşı & Balık, 2003; Barlas & Dirican, 2004; Ekmekçi & Kırankaya, 2006).

In the region, semi-arid climate conditions prevail and it is characterized as rainy/snowy winter and hot dry summer. The dry period in the region is from June to September (Fig. 5.4.). Average precipitation and air temperature are 405±80 mm and 11.9±8.4°C in terms of thirty one year's data (1980-2011) obtained from Turkish State Meteorological Service (2011). Generally, lakes were covered with ice during winter.

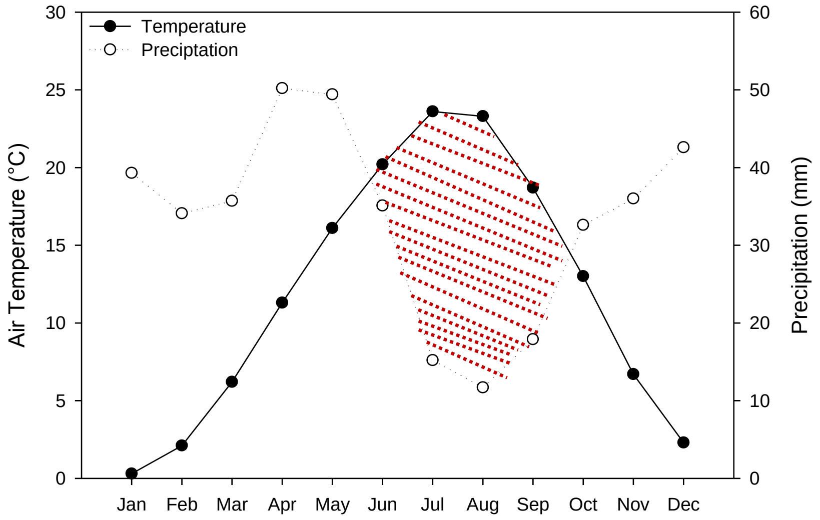

Figure 5.4. Climate diagram for studied region. Red dotes represented the dry period.

5.2.2. Sampling

From 1997 to 2011, water samples were taken biweekly during the growing season, monthly outside the growing season and no sample was taken during the ice periods. All physical and chemical parameters were taken from the deepest point of the lakes. From 1997 to 2007, the dissolved oxygen and temperature measurements were performed at half meter increments using WTW oxygen meter and salinity and conductivity were measured by using Orion conductivity meter. Since 2007, conductivity (±1 µS cm^{-1}), pH (±0.1), salinity (±2 mg chloride L^{-1}), temperature (◦C), dissolved oxygen (mg L^{-1}) were measured by using YSI 556 multiprobe oxygen meter. Water samples for chemical analyses including total phosphorus (TP), total nitrogen (TN), soluble reactive phosphate (SRP), alkalinity and chlorophyll *a* (Chl *a*) and biological variables (zooplankton) were taken from depth-integrated, mixed samples (40L) from the entire water column by using a KC Denmark Water Sampler (3.5 L) from 2007 to present day. Before 2007, integrated water samples were taken from the epilimnion by using a tube sampler. Samples for chemical analysis were kept frozen until analyses.

Samples for chemical analysis were frozen until analyses. For TP, the acid hydrolysis method was used (Mackereth, Heron & Talling, 1978). For TN analysis, which was not analysed before 2007, Scalar Autoanalyzer Method was used (San++ Automated Wet Chemistry Analyzer, Skalar Analytical, B.V., Breda, Netherlands). The chlorophyll *a* was determined using ethanol extraction (Jespersen & Christoffersen, 1987) and the absorbance measured at 663 and 750 nm.

Before 2007, the 45 µm mesh sized nylon plankton net was used since then 20L of water (out of 40L mixed sample) were filtered with a 20 µm mesh size filter. Zooplankton samples were fixed within 4% lugol solution. All zooplankton taxa were identified to genus or species level whenever possible and counted 50-100 individuals of the most abundant taxa.

Countings were performed at the magnification of X40 (cladocera and copepods) in a stereomicroscope (LEICA MZ 16) and X60 (rotifers) in an inverted microscope (LEICA DMI 4000). For taxonomical identification, the keys developed by Scourfield ve Harding (1966), Ruttner-Kolosko (1974), Pontin (1978), Einsle (1993), Segers (1995), Smirnov (1996), Flö*β*ner (2000), Smith (2001) were used.

Fish samplings were performed with multi-mesh gill nets before 2007 using 100m length and 3.5m height comprising ten different mesh sizes (knot to knot) of 7, 9, 12, 16, 22, 25, 36, 42, 55 and 65 mm were used. However since 2007, fish sampling was performed with multi-mesh Lundrens gill nets (length 30 m; height 1.5 m; 12 panels with mesh sizes (knot to knot) of 5.0, 6.25, 8.0, 10.0, 12.5, 15.5, 19.5, 24.0, 29.0, 35.0, 43.0 and 55.0 mm), number of set used depended on the lake size. The nets were set overnight both parallel to the littoral and open water zone of the lake for an average duration of 12 hours. Total length and weight of the fish was measured.

Percent aquatic plant covers of lakes were estimated via floating-leaved and submerged macrophyte data along the parallel transect lines depending on lake size. On the other hand, Percent Plant Volume Inhabited (PVI %) was calculated from the %PVI= (%c * p) /wd, where c : plant coverage, p:average plant height and wd: water depth.

The lake water level and meteorological data were obtained from the General Directorate of Electrical Power, Resource Survey and Development Administration (EİE, 2011), and Turkish State Meteorological Service (MGM, 2011), respectively.

5.2.3. Statistical analyses

To identify the periods, z-score, which is a useful statistical method for standardizing large data sets (Gerten & Adrian, 2000), were calculated. First subtract the mean obtained from observation and then divide the residual by the standard deviation of all data. If the z-score of was above zero the observation referred as “high water level (HWL)” whereas if the value below zero than the observation referred as “low water level (LWL)”. To compare the characteristics of zooplankton community composition, main limnological characteristics during low water level and high water level, periods nonparametric Kruskal-Wallis One-Way ANOVA was used. Furthermore, linear regression was conducted to evaluate the interactions among variables. Sigma Stat 3.5 was used for the statistical analyses. The long-term monitoring of these two lakes have been conducted since 1997 by METU Limnology Laboratory under the supervision of Prof.Dr. Meryem Beklioğlu Yerli. Thus, physical, chemical and biological data were obtained from the METU, Limnology Laboratory. The dataset were already used for different purposes (e.g. mesocosm experiments, analyses of biomanipulation, plant developments etc.) by several M.Sc. students which carried out their thesis at METU Limnology Laboratory. Furthermore, the dataset will be used in the PhD/M.Sc. thesis students who will carry out their thesis at METU Limnology Laboratory.

5.3. Results

To identify the periods, z-score, were calculated. First subtract the mean obtained from observation and then divide the residual by the standard deviation of all data. If the z-score was above zero the observation referred as “high water level (HWL)” whereas if the value below zero than the observation referred as “low water level (LWL)”. Thus, 2001, 2005-2009 was the low water level period and the rest of the years were high water level period (Fig. 5.5.).

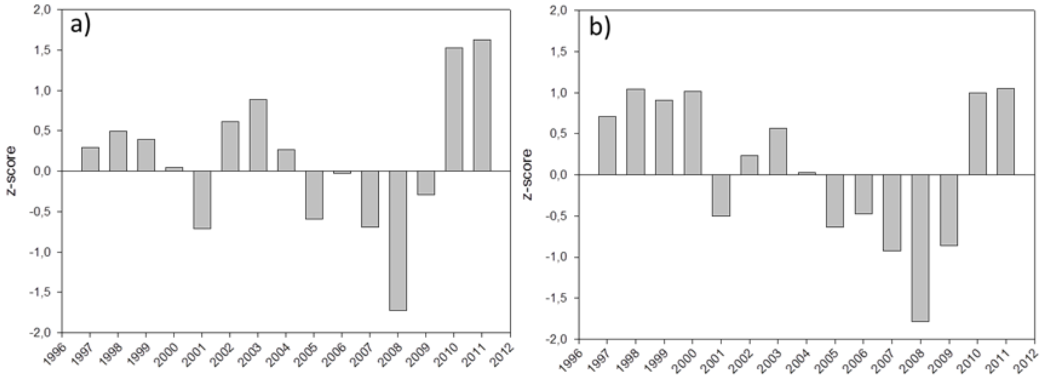

Figure 5.5. Low and High water level periods according to z-score value in Lakes a) Mogan b) Eymir.

5.3.1. Environmental variables

There were two periods observed according to the water level fluctuation in lakes. During the low and high water level periods; water clarity, nutrient displayed significant differences whereas plant coverage and fish assemblages of lakes did not significant (Table 5.1). Mean±SD of variables in Lake Mogan and Eymir from 1997 to 2011 during high and low water level periods were given in Appendix D.

Table 5.1. Kruskall-Wallis one-way ANOVA results in two lakes comparing high water level (1997-2000, 2003, 2004, 2010, and 2011) and low water level periods (2001,2005- 2009).

	Mogan	Eymir
Salinity (‰)	***<0.001***	***<0.001***
Secchi depth (m)	***<0.001***	ns
Chlorophyll *a* (µg L^{-1})	ns	ns
Suspended solid (mg L^{-1})	***<0.001***	***<0.001***
Total dissolved solid	***<0.001***	***<0.001***
Total Phosphorus *a* (µg L^{-1})	***<0.05***	<0.1
Soluble Reactive Phosphorus *a* (µg L^{-1})	***<0.001***	<0.1
Dissolved Inorganic Nitrogen(µg L^{-1})	ns	***<0.001***
Nitrate+ Nitrite (µg L^{-1})	ns	***<0.001***
Ammonium (µg L^{-1})	ns	***<0.01***
Dissolved oxygen (mg L^{-1})	<0.1	ns
Fish	ns	ns
PVI	ns	ns

Throughout the years the water level fluctuated in both lakes especially in 2008 when the decrease of the water level was notable. Decreasing water level triggered an increase in salinity in lakes; meanwhile salinity was low from 1997 to 2000 when water levels were high.

In 2001, the water level dropped significantly and salinity started to increase however, as the water level recovered on the following year and the increase in salinity concentration remained below the average of dry periods (1.21± 0.0 and 1.20± 0.0 in Lakes Mogan and Eymir, respectively).

The water level and salinity were inversely correlated in Lakes Mogan and Eymir ($r^2=0.38$, $p<0.05$; $r^2=0.29$, $p<0.05$; respectively) though the salinity increased ca. 2 fold that reached to 2.5 ‰ and 2.05 ‰ in both lakes throughout the second prolonged low water period between 2005-2009, respectively (Fig. 5.6). (Table 5.1).

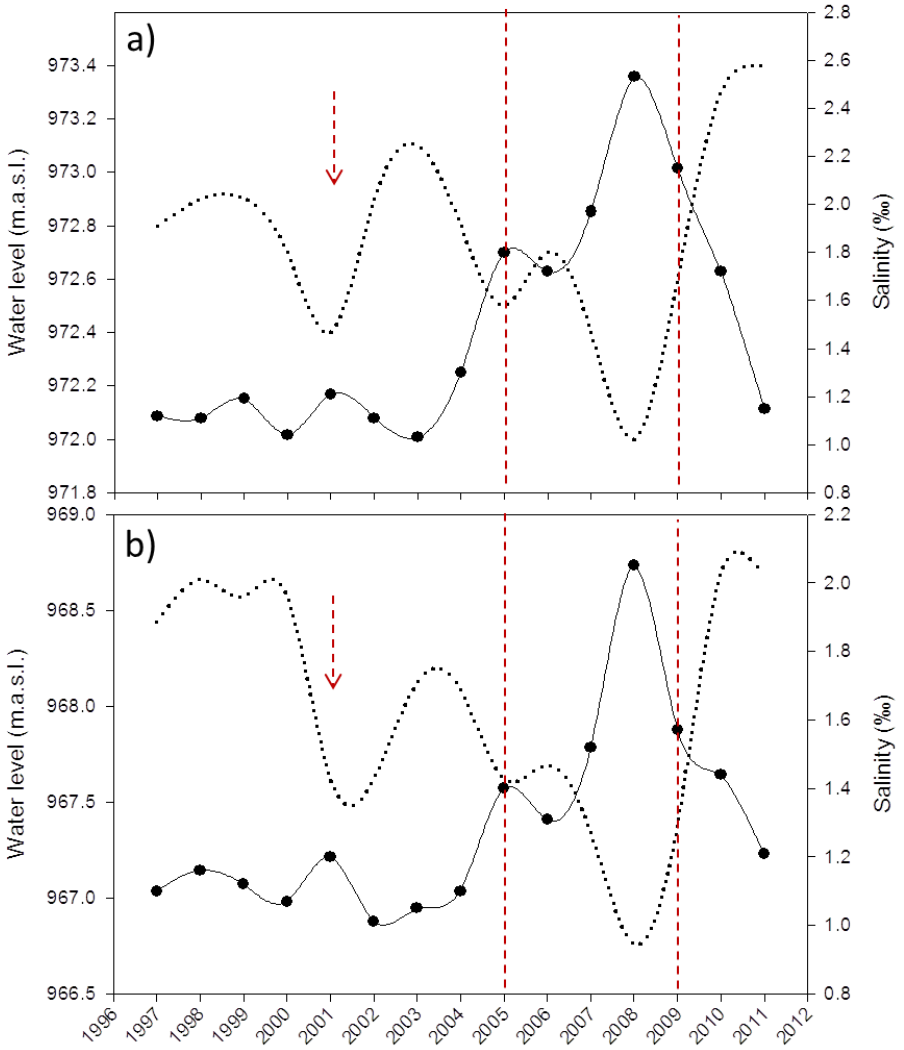

Figure 5.6. Water level (dashed lines) and Salinity (solid lines with standard error) in Lakes a) Mogan and b) Eymir from 1997 to 2011. Intervals of vertical red dashed lines and arrow indicate the low water level period.

The upstream Lake Mogan, Secchi depth was high during high water level period in contrast suspended solid, were low (Table 5.1). Whereas in Lake Eymir: Secchi depth and chlorophyll *a* concentration did not display significant difference between periods.

The average Secchi (±SE) depths in Lakes Mogan and Eymir were 1.40± 0.1m and 1.81 ±0.1 m, respectively throughout the study period. In Lake Mogan, the highest water clarity was observed in 1997 while the lowest Secchi depth transparency (0.55± 0.7m) was observed in 2008 which was the lowest observed water level year. Likewise, the highest Secchi depth (2.82±0.2 m) was observed in 1999-2000 (1st biomanipulation and following year) while lowest transparency (1.04± 0.2 m) was observed during low water level (LWL) period particularly in 2008 (despite 2nd biomanipulation has still continued) in Lake Eymir (Fig. 5.7). Concurrently, there were negative correlation between Secchi disc transparency and chlorophyll a concentration in Lakes Mogan and Eymir (r^2= 0.30, p<0.001; r^2= 0.37, p<0.001, respectively). Furthermore, the concentration of suspended solid was also high during the low water level period in the both lakes thus it might have contributed to lower Secchi depth observed in the low water periods (Table 5.1). However, chlorophyll a concentration did not display significant correlation with water level in lakes. Furthermore, the chlorophyll a concentration of lakes displays bimodal peaks in early spring and late summer.

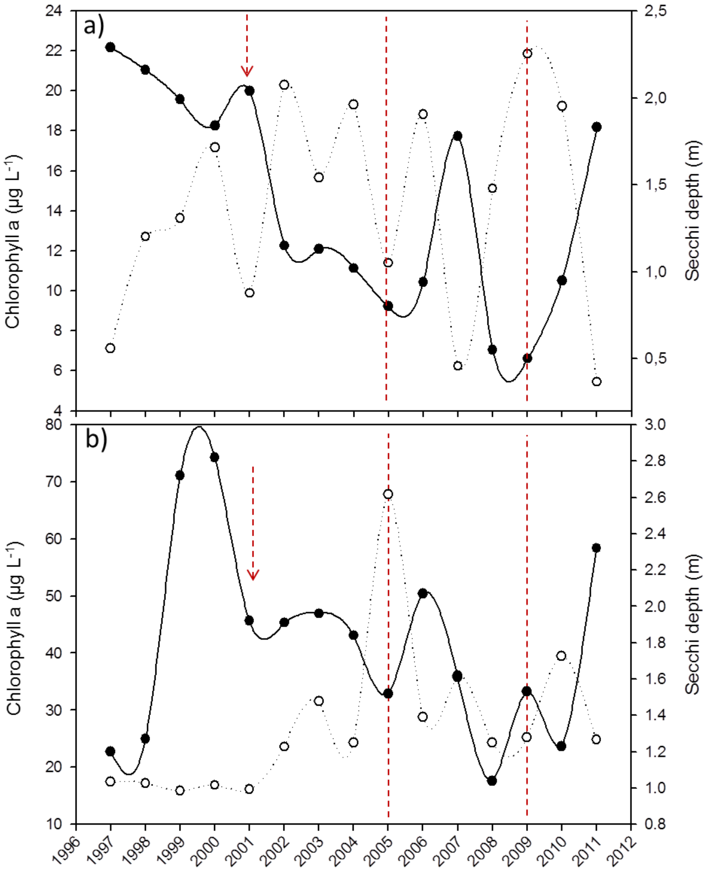

Figure 5.7. Secchi depth (fiiled circle) and chlorophyll *a* (open circle) in Lakes a) Mogan, b) Eymir from 1997-2011. Intervals of the vertical red dashed lines and arrow indicate the low water level period.

The dissolved oxygen concentration did not display significant difference between periods in lakes. The average dissolved oxygen concentration in Lakes Mogan and Eymir were 7.31±1.7 and 5.52±1.5 mg L^{-1}, respectively.

The oxygen concentration tended to decrease from 2005 to 2009 which was cover low water level period (Fig 5.8). The oxygen concentration below 5-6 mg L^{-1} assumes shortage of oxygen in freshwater (Richards, 2011).

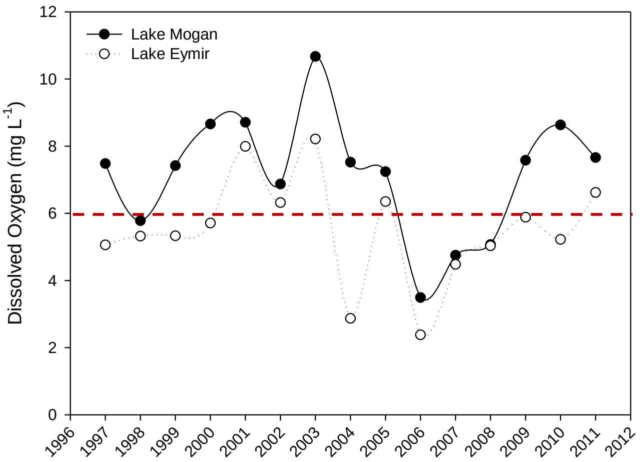

Figure 5.8. Changes in dissolved oxygen (mg L^{-1}) in lakes. Red das line indicates critical level.

There were positive correlation between TP and SRP in Lakes Mogan and Eymir ($p<0.05$, $p<0.0001$, respectively) (Fig. 5.9). In Lake Mogan, the highest TP concentration (140±0.94 μg L^{-1}) was recorded in 2008 and decreased gradually afterwards (Fig. 39).

Moreover, SRP was also recorded high (ca.40 μg L^{-1}) in 2007-2008 and decreased gradually as observed in TP (Fig. 5.9). Thus during LWL period TP and SRP concentrations were high (Table 5.1).

Meanwhile, the concentrations of TP and SRP in Lake Eymir reached the highest value (ca. 480 μg L^{-1} and 370 μg L^{-1}, respectively) in 2004- 2005 (before the 2nd biomanipulation) and decreased gradually since 2007 and in 2011 the lowest concentration of throughout the study period (105.2 ±1.4 µg L^{-1}) was observed.

However TP and SRP concentration did not display significant difference between low and high water level period (Table 5.1). Furthermore, the concentrations reached to the highest level during summer (June-August) in Lake Eymir indicating at internal summer phosphorus release, whereas in Lake Mogan did not display any seasonal variation pattern.

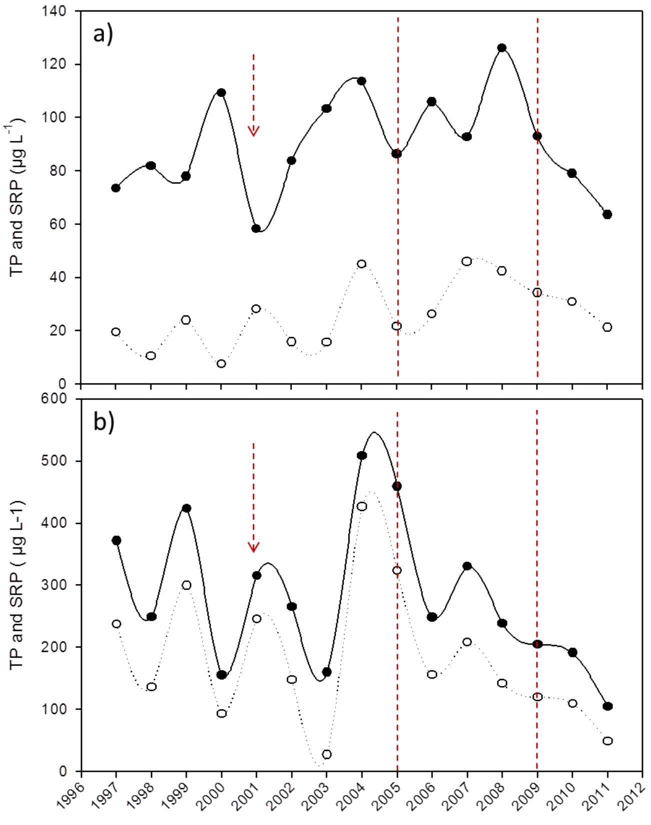

Figure 5.9. Annual mean of total phosphorus (TP) and soluble reactive phosphate (SRP) concentrations in Lakes: a) Mogan, b) Eymir from 1997 to 2011. Filled circles: TP, open circles: SRP. Intervals of the vertical red dashed lines and arrow indicate the low water level period.

The in-lake DIN concentration in Lake Mogan reached the highest value in 2003 (Fig. 5.10.). The in-lake DIN concentration in Lake Mogan mostly consisted of ammonium from 1997 to 2004 and following years the contribution of nitrate concentrations displayed increasing trend (Fig. 5.10.). The in-lake DIN, NOx-N and NH_4-N did not display significant difference between low and high water level period in Lake Mogan (Table 9). Meanwhile the concentrations were high during low water level periods in Lake Eymir. Furthermore, the in-lake DIN concentration reached the highest value (1095±4.5 µg N L^{-1}) in 2008 consisting of high ammonium concentration.

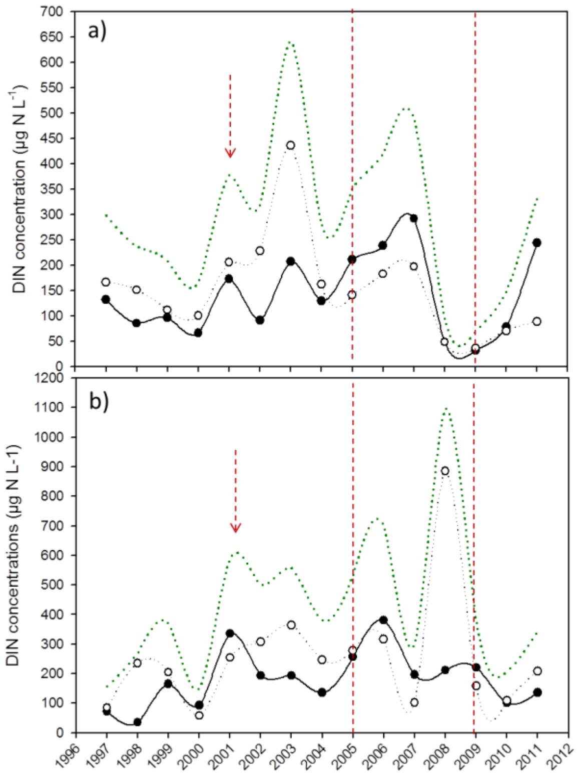

Figure 5.10. Annual mean of Dissolved inorganic nitrogen concentrations in Lakes: a) Mogan, b) Eymir from 1997 to 2011. Filled circles: NO_x-N, open circles: NH_4-N, green dot: DIN Intervals of the vertical red dashed lines and arrow indicate the low water level period.

The DIN and SRP ratio was given Fig. 5.11. From 1997 to 2011 in Lake Mogan, the ratio was much higher than in Lake Eymir. Except for in 2003, the ratio was observed <10 in Lake Eymir.

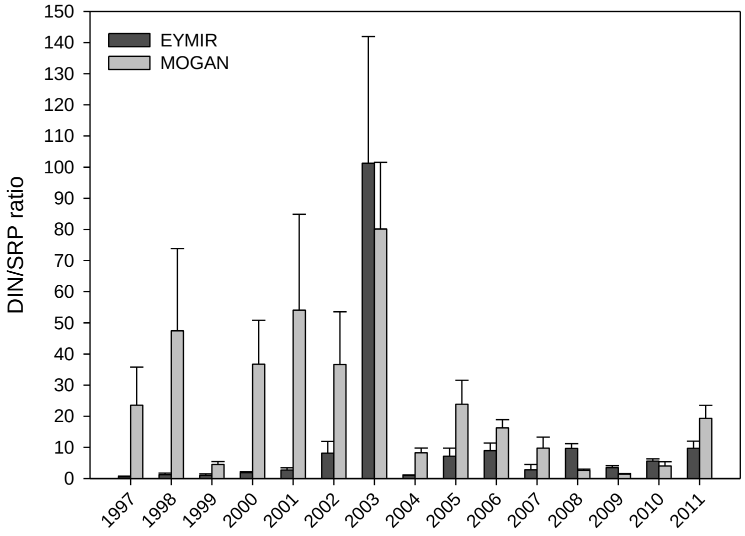

Figure 5.11. Changes in DIN: STP ratio in lakes from 1997 to 2011.

Furthermore, total nitrogen (TN) analysis was performed since 2007. 2008 onward, TN has display decreasing trend and reached the lowest concentration in 2011 which was the high water level period in Lake Eymir whereas in lake Mogan. TN concentration reached to the highest concentration in 2010 than decreased again. The TN: TP ratio of the lakes displayed decreasing trend since 2011 the lakes displayed N-limitation. (Fig. 5.12.).

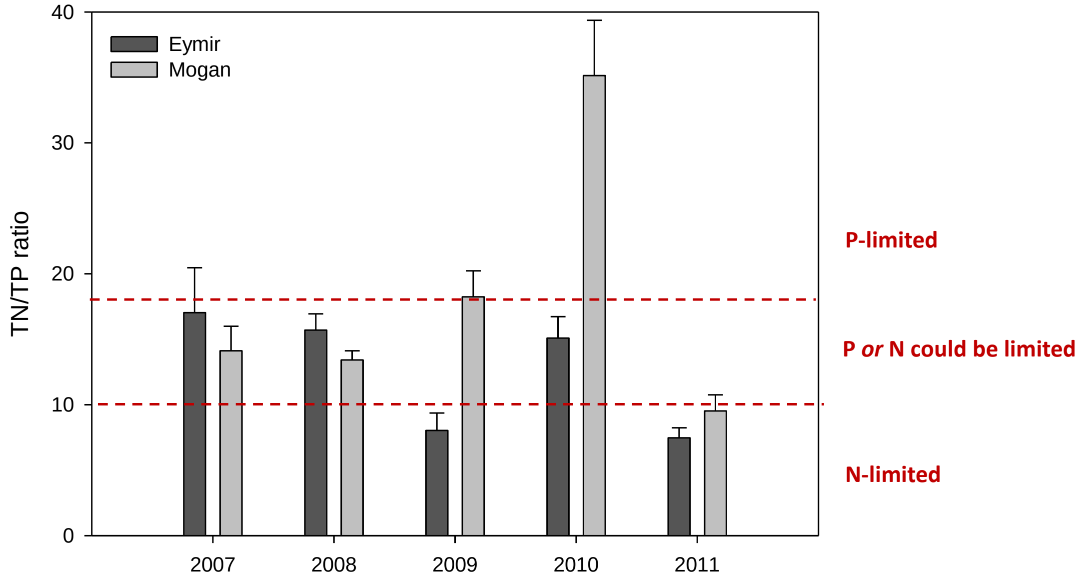

Figure 5.12. TN:TP ratio of Lakes Mogan and Eymir.

In Lake Mogan, despite there was no quantitative data from 1997 to 2000, the lake had extensive submerged plant coverage ca. 80% PVI consisting of *Potemogeton pectinatus* L. and *Chara* sp. (Beklioğlu personal observation). From 2001 to 2003 the submerged plant coverage was ca. 50% PVI and following years the coverage declined. Concurrently, the Secchi depth also declined and the water level increased. After the decrease in water level promoted the plant development and the coverage reached 40% in 2005, however, increased WL in subsequent year lower the plant coverage again. In 2008, when the water level was detected to be lowest, the submerged plant coverage was one of the highest recorded (62%) with consisting of *Potemogeton pectinatus* L. and *Najas marina* L. With the onward 2010 increasing water level the plant coverage decreased again (Fig. 5.13). However there was no significant relation observed between chlorophyll *a* concentration and PVI % as well as water level during the study period in Lake Mogan (r^2=0.33; p<0.1).

In Lake Eymir, upon biomanipulation, submerged plants increased in the lake, the highest submerged macrophyte coverage (76%) was observed in 2000 and decreased gradually during the study period. *Potamogeton pectinatus* L. and *Ceratophyllum demersum* L. had high coverage moreover *Myriophyllum spicatum* L., *Chara* sp. and *Najas* spp. (*Najas minor/marina*) were found with very low PVI% (see Beklioğlu & Tan, 2008). However, onward 2005 to present there was no major changes observed in PVI% in Lake Eymir. Furthermore, submerged plant was negatively related with the chlorophyll *a* as well as water level ($r^2= 0.37$, $p<0.05$; $r^2=0.29$, $p<0.05$, respectively).

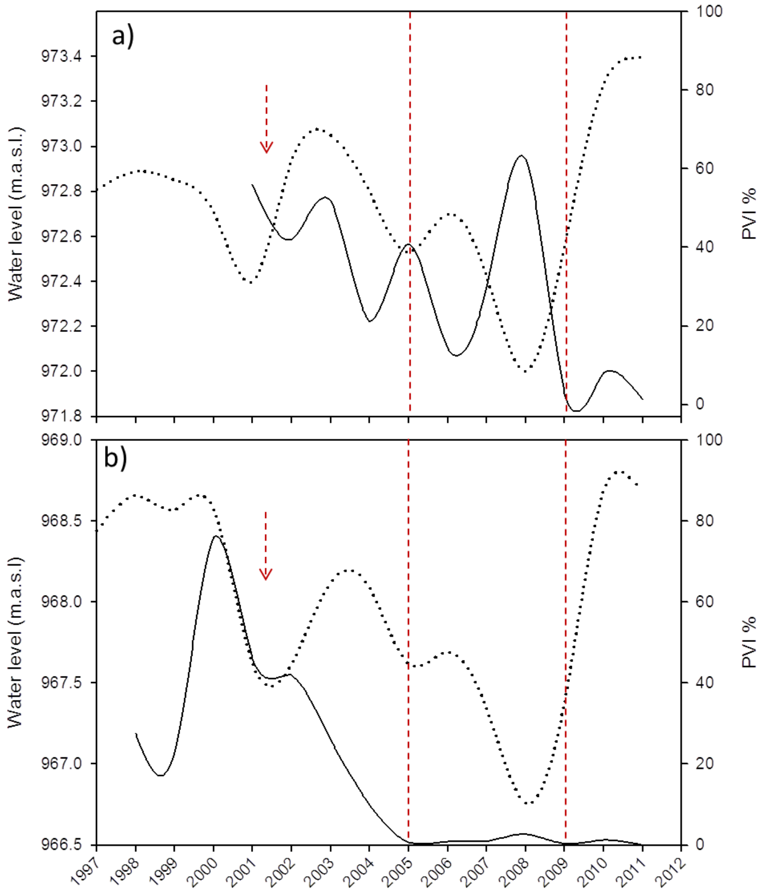

Figure 5.13. Plant Volume Infested in Lakes a) Mogan, b) Eymir from 1997 to 2011. Water level (dashed lines) and PVI % (solid lines). Intervals of the vertical red dashed lines and arrow indicate the low water level period.

5.3.2.Fish Assemblage

Fish did not display any significant differences between periods however in Lake Mogan there were not enough fish data to investigate the effect. Furthermore, in Lake Eymir the second biomanipulation has still continued since 2006 which covers both low water level and high water level period though the fish density did not display significant differences between periods (Table 5.1).

For Lake Mogan, existing fish data were from 2007 to 2011 (Fig. 5.14). The fish community composed of mostly Cyprinidae family carp, tench, pike, *Alburnus escherichii*, Steindachner 1879, *Cobitis taenia*, Linnaeus 1758 (spined loach) and invasive topmouth gudgeon. However, the size of the carp (15.6±0.2cm) and tench (11.9±1.5cm) was not very large. On the other hand, the density of <10 cm fish (*P. parva* and *A. escherichii*) was observed to be high. High fish density might have caused the decrease in water clarity despite the interaction did not significant but display inverse relationship. In 2008 and 2009, the Secchi depth was low while the fish density was observed to be high and the opposite was observed in in 2007 and 2010.

In Lake Eymir, there have been two biomanipulation periods: first one 1998-1999 and the second one has continued since 2006 (Fig. 5.15.). During the study years carp, tench, pike, *A. escherichii*, topmounth gudgeon and young of the year (Y-O-Y) were caught (Fig. 5.15). After first biomanipulation, carp and tench were decreased concurrently the density of small sized bleak and the Y-O-Y increased remarkably (Fig. 5.15) but the biomass was very low ca. 17 kg. net^{-1} night^{-1}. Furthermore, tench reached to the highest density (145.6±1.7g) in 2003, which was roughly the same level as pre-biomanipulation period. The density of pike increased immediately afterwards the first biomanipulation decreased gradually towards 2003 when was the last pike record along years. In 2006 the second biomanipulation started and it still currently continues.

The density of large carp and tench displayed decreasing trend as observed in the second pre-biomanipulation period. In contrast, small sized bleak, Y-O-Y and exclusively invasive species topmouth gudgeon (*P. parva*) increased.

The amount of fish removed by fisherman during 2nd biomanipulation showed the highest fish catch (tench and carp) was in 2008 (Fig. 5.14).

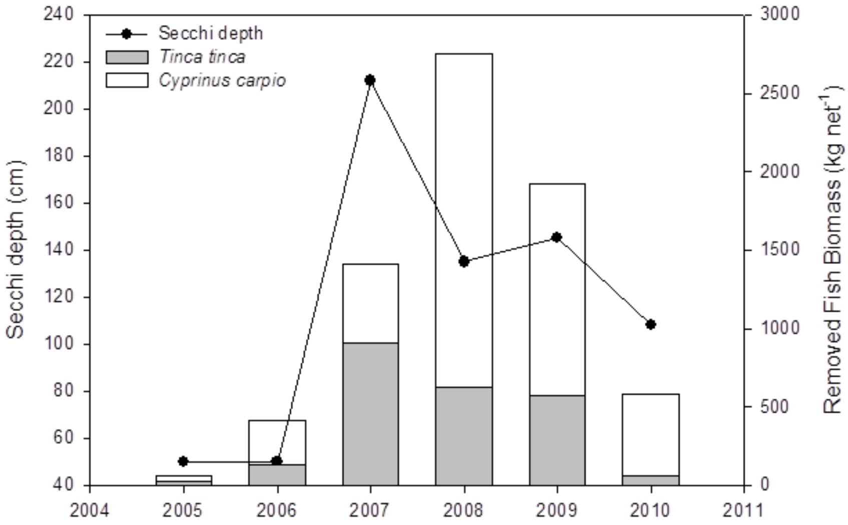

Figure 5.14. Removed fish biomass and Secchi disc transparency during second biomanipulation period (data taken from the fisherman).

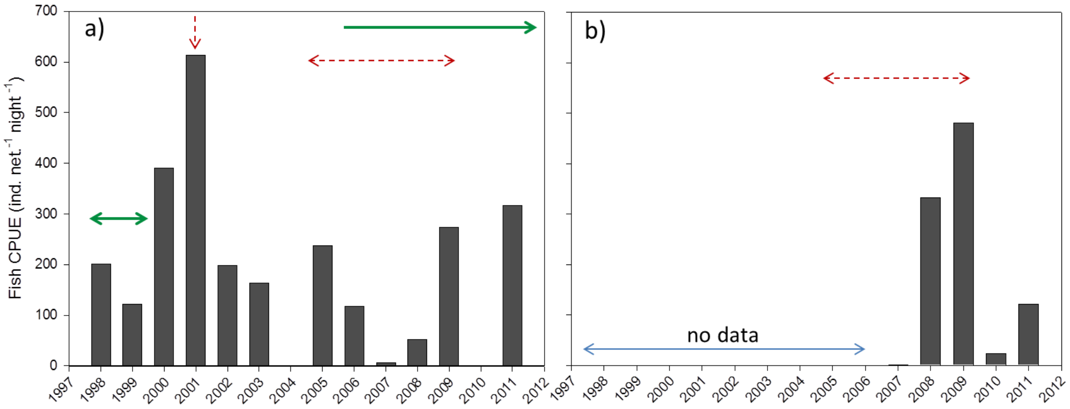

Figure 5.15. Changes in fish density in Lakes a) Eymir, b) Mogan. Green arrow: biomanipulation periods, red arrow: low water level periods.

5.3.3. Zooplankton Community Composition

Zooplankton community composition was compared during high and low water levels period for Lakes Mogan and Eymir (Table 5.2). Between high and low water period, salinity and nutrients increased during the low water level period that had spectacular effect on the community composition of zooplankton (Table 9). Small cladocerans included pooled biomass of *Chydorus sphericus* (O.F. Müller, 1776), *Bosmina longirostris* (O.F. Müller, 1785), *Alona* sp. and *Pleuroxus* sp. because the density of these species were very low though the contribution of total biomass was also low in the lakes.

In Lake Mogan, biomass of total rotifer, *Filinia longiseta* (Ehrenberg, 1834), *Brachionus* spp.(*B. Angularis* Gosse, 1851, *B. calciflorus* Pallas, 1766, *B. quadridentatus* Hermann, 1783) and *Asplanchna* sp. were significantly high during the high salinity period whereas *Daphnia longispina* O.F. Müller, 1875 was observed high during low salinity period. However, the largest sized *Daphnia magna* (Straus, 1820) did not display significant difference between saline (LWL) and non-saline (HWL) periods furthermore, there were positive correlation between salinity which was observed during low water level period, and *D. magna* (r^2=0.27, $p<0.05$) as well as total rotifer biomass (r^2= 0.58, $p<0.05$) (Fig 5.16.). Furthermore, despite *Diaphanasoma* was not exhibit significantly different between periods, highest biomass was observed during saline period (Fig 5.16.). In addition, other environmental variables (TP, DIN, SS etc.) did not display any significant correlation between zooplankton groups in Lake Mogan between periods. However, Cladocera was inversely related with Chl a concentration throughout the year ($p<0.05$).

Meanwhile, in Lake Eymir, the biomass of *D. magna* and *Polyarthra* sp. was observed high during saline low water level period whereas *Ceriodaphnia* sp. *Keratella quadrata* (Müller, 1786) and naupli displayed opposite pattern (Table 5.2). Despite biomass of total cladoceran and total copepod did not display significant correlation between periods, total cladocerans and total copepods displayed positive relation with salinity (r^2=0.70, <0.001, r^2=0.26, $p<0.05$).

On the other hand, *Daphnia* display negative correlation between Chl *a* concentration during study period (r^2=0.25, $p<0.001$).

In 2008, the ratio of Daphnia:Chl a was observed to be high due to the high abundance of large sized *Daphnia magna,* contrary to expectation the Secchi disc transparency was not high. During low water level period DIN concentration was high accordingly the biomass of total cladocera also displayed positive relation with DIN (r^2=0.1, $p<0.001$) however there was no significant correlation with the other environmental variables and the zooplankton group.

Table 5.2. Kruskall-Wallis one-way ANOVA results in two lakes comparing high water level with low salinity (1997-2000, 2003, 2004, 2010, and 2011) and low water level with high salinity periods (2001,2005- 2009) on zooplankton biomass.

	Mogan	Eymir
Cladocera total	0.15	0.22
Copepoda total	0.71	0.05
Rotifera total	***<0.001***	0.88
Daphnia longispina	***<0.05***	-
Daphnia pulex	**-**	0.24
Daphnia magna	0.27	***<0.01***
Ceriodaphnia sp.	0.47	***<0.001***
Diaphanasoma sp.	0.82	0.07
Small cladocerans	0.62	0.06
Arctodiaptomus bacillifer	0.35	0.23
Cyclops sp.	0.23	0.32
Naupli	0.22	***<0.05***
Keratella quadrata	0.47	***<0.05***
Brachionus spp.	***<0.05***	0.75
Filinia longiseta	***<0.05***	0.36
Asplanchna sp.	***<0.01***	0.18
Hexarthra spp.	few	0.12
Polyarthra spp.	few	***<0.05***

The dominant cladocerans were large sized *Daphnia magna* and *Daphnia longispina* in Lake Mogan however *Ceriodaphnia* sp. and *Diaphanasoma lacustris* (Korinek 1981) had also high contribution to the total cladoceran biomass. Small sized *Chydorus sphericus*, *Bosmina longirostris* and *Alona* spp. (*A. rectangula* Sars, 1862 and *A. affinis* Leydig, 1860) had very low biomass.

Throughout the study periods, *D. magna*, *D. longispina* and *Diaphanasoma* reached the maximum biomass in 2008 which was the highest salinity year. However the coexistance of large and medium sized species display seasonal differences mentioned below. Furthermore, between 1999 and 2000 the cladoceran community consisted of small cladocerans and medium sized *Ceriodaphnia* and *Diaphanasoma* (Fig. 5.16). However, during this period calanoid copepod *Arctodiaptomus bacillifer* (Koelbel, 1885) was observed with high biomass whereas Cyclops were relatively low and *D. magna* was also recorded (Fig. 5.16; 5.18). Furthermore, the biomass of calanoid copepod was high mostly during low water level period despite there were no statistical difference between periods (Table 5.2).

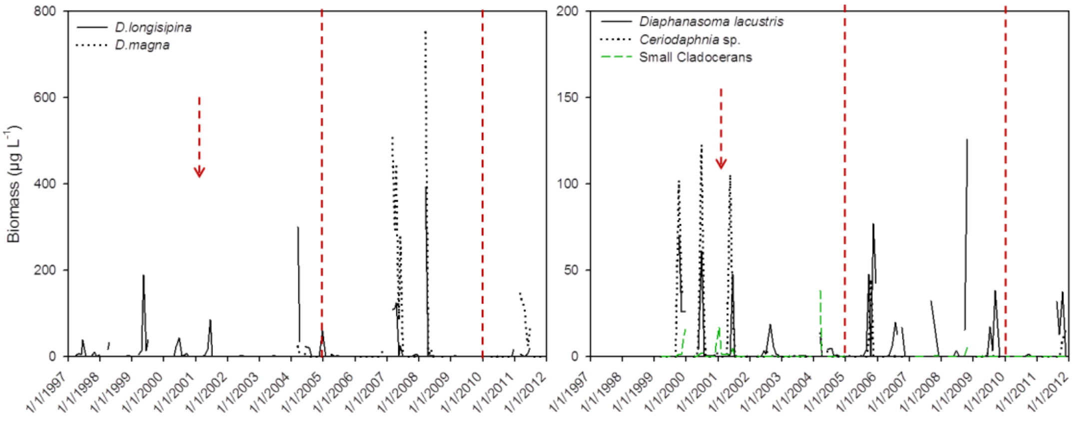

Figure 5.16. Biomass of zooplanton species in Lake Mogan from 1997 to 2012. Intervals of the vertical red dashed lines and arrow indicate the low water level period.

Througout the study period, cladocerans species displayed seasonal variation such as spring peak in *D. magna* and *D. longisipina* (Fig. 5.17). Furthermore, *Ceriodaphnia* and *Diaphanasoma* display bimodal pattern with two highest values in June and October (Fig. 5.17).

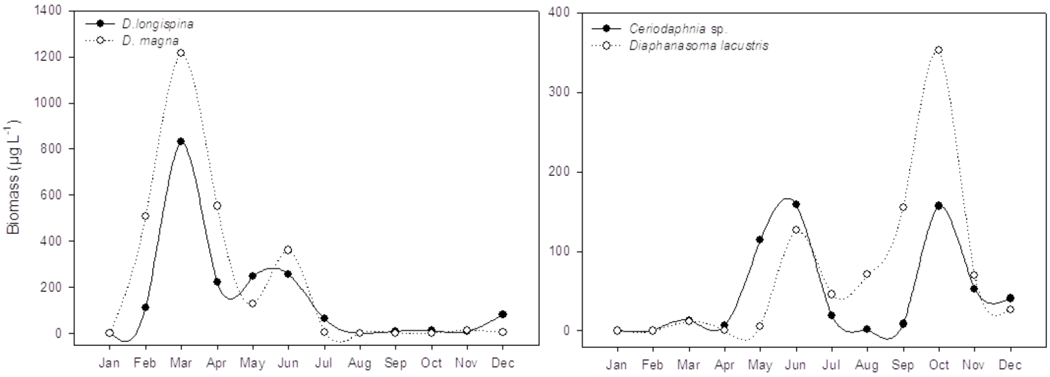

Figure 5.17. Seasonal changes in dominant Cladocera species in Lake Mogan.

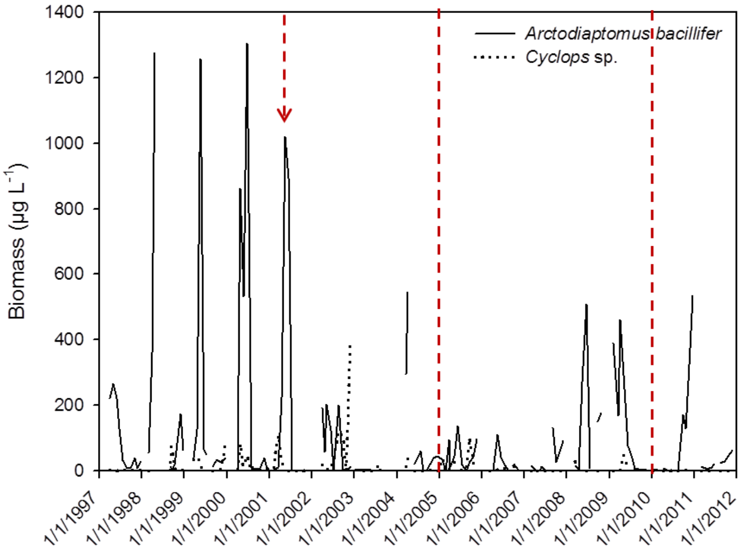

Figure 5.18. Biomass of Copepod species in Lake Mogan from 1997 to 2012. Intervals of red dash line and arrow indicated the low water level periods.

Furthermore, *Arctodiaptomus bacillifer* and *Cyclops* sp. were found in every month but reached the highest biomass during spring and autumn (bimodal), respectively. Naupli and copepodites were also display bimodal distribution pattern with two peaks in April and October during study period.

The rotifera species only identified onward 2004 to the present thus the obtained data mostly cover the high saline (LWL) period. During the study period, *Keratella quadrata*, *Filinia longiseta* and *Asplanchna* sp. were dominant in the lake (Fig. 5.19). In addition, *Brachionus* spp. (*B. angularis*, *B. calciflorus*, *B. quadridentatus*), *Polyarthra* spp., *Hexarthra* spp., *Anureopsis fissa* Gosse, 1851, *Notholca acuminata* Carlin, 1943 and *Lecane* spp. were also present during the study period but with very low biomass.

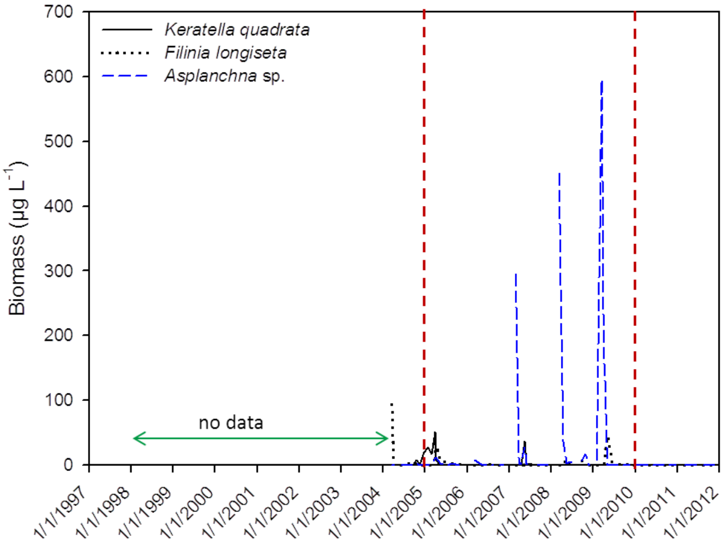

Figure 5.19. Biomass of dominant rotifer species in Lake Mogan from 2004 to 2012. Intervals of red dash line indicated the low water level periods.

The contribution of total zooplankton was mostly consisted of copepods however in 2007 the contribution of copepods decreased remarkabley during the high saline conditions were prevailing and shifted to the dominancy of cladoceran. Furthermore, in 2009 the rotifer biomass which was consisting of *Asplanchna* sp. increased onward and decreased to 1% of total zooplankton (Fig. 5.20).

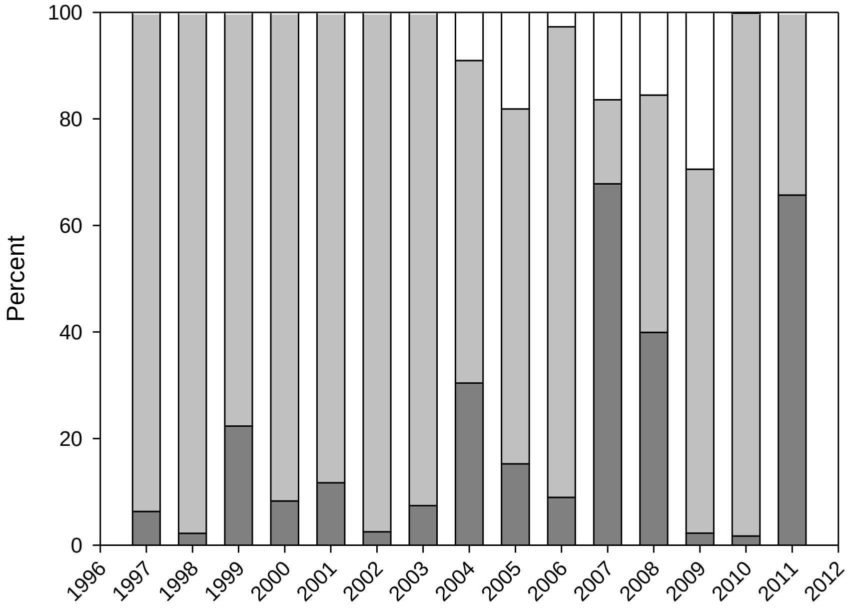

Figure 5.20. Percent of zooplanton groups in Lake Mogan from 1997 to 2011. Dark grey: Cladocerans, light grey: Copepods and white: Rotifers. Note that no rotifer data before 2004.

In downstream Lake Eymir large-sized *D. magna* and *D. pulex* were the dominant cladoceran species. The other cladocerans recorded in the lake were *Diaphanasoma brachyurum, Ceriodaphnia* sp. and low biomass of small sized *Chydorus sphericus, Bosmina longirostris*, *Alona* sp. and *Pleuroxus* sp.

Among the species *D. magna* displayed significant increase during the low water level period which was the high salinity concentration as well as low fish predation period due to the second fish biomanipulation which was initiated onward 2006, in comparison to *D. pulex* which did not display any trend (Fig. 5.21; Table 5.2).

The peak in *D. magna* recorded in 2001, when salinity was high, was lower than that of in 2008. Probably because of reduced fish predation through second fish biomanipulation. Furthermore, among cladoceran species *D. magna* and salinity had positive interaction ($r^2= 0.2$, $p<0.001$). The chlorophyll a concentration and *Daphnia* biomass were negatively correlated though it was critical but not significant ($p<0.1$).

Moreover, *Ceriodaphnia* were found in low salinity with high water level period whereas *Diaphanasoma* and small cladocerans did not display a significant difference between low and high water level period (Fig. 5.21, Table 52). However *Diaphanasoma* had high biomass at the end of 2009.

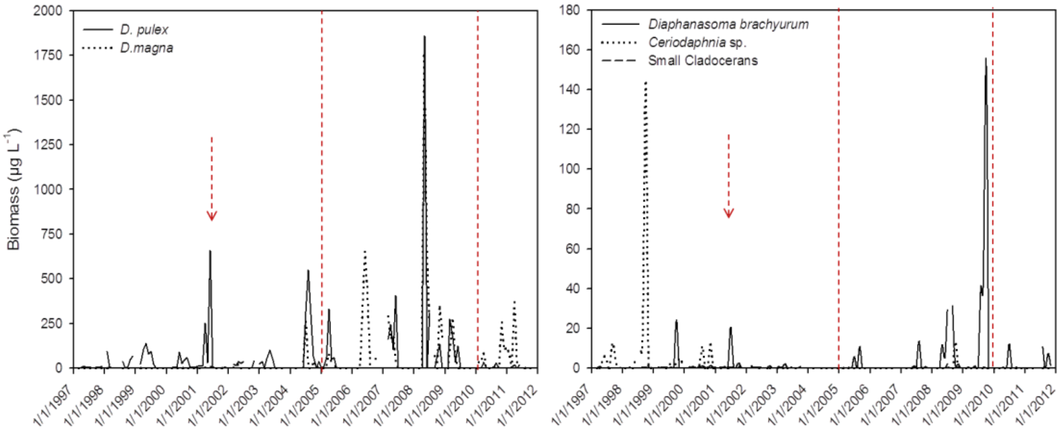

Figure 5.21. Biomass of zooplanton species in Lake Eymir from 1997 to 2012. Intervals of red dash line and arrow indicated the low water level periods.

During spring (April to June) the biomass of *D magna* and *D. pulex* were high (Fig. 5.22). Further *D. magna* showed two small peaks including summer and autumn whereas D.pulex showed the clasical small autumn peak. Unlike the large cladocerans, *Diaphanasoma* and *Ceriodaphnia* showed highest peak on October though *Diaphanosoma* had a smaller summer peak (Fig. 5.22). However, small sized cladocerans did not show any specific seasonality.

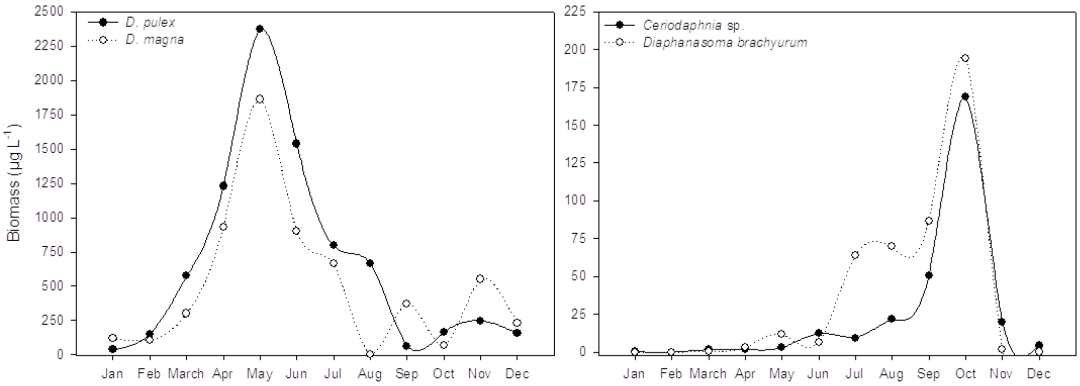

Figure 5.22. Seasonal changes in zooplankton species. Note the different scale.

Copepods were represented by two group calanoid *Arctodiaptomus bacillifer* and cyclopoid *Cyclops* sp. Neither *A. bacillifer* nor *Cyclops* sp. had significant relationship with the environmental variables (Fig. 5.23). However, in 2008 which was the lowest water level period with the highest salinity, there was high *A. bacillifer* biomass observed during spring to mid-summer. However, *A. bacillifer* did not display significant difference during periods (Table 10). Furthermore, the highest biomass of Cyclops sp. was observed during winter to mid-spring especially in 2004. The density of nauplii was significantly higher during the non-saline (HWL) period and found in each month (Table 5.2).

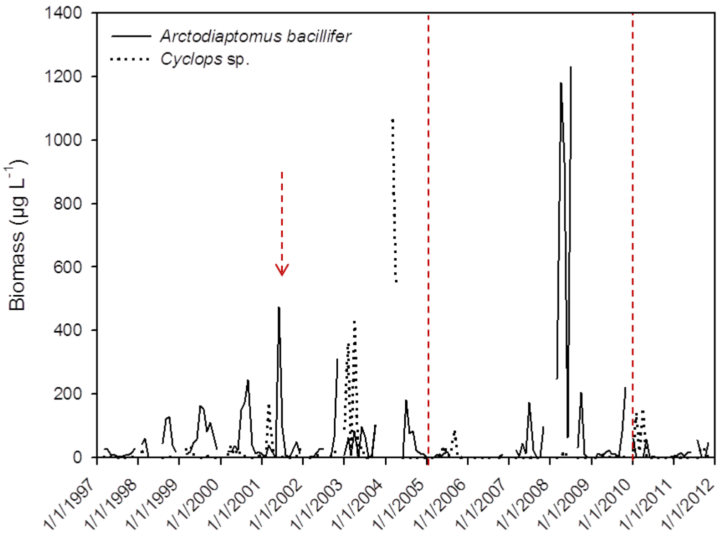

Figure 5.23. Biomass of Copepoda species in Lake Eymir from 1997 to 2012. Intervals of red dash line and arrow indicated the low water level periods with high salinity.

The biomass of Rotifera was dominated by *Keratella quadrata*, *Brachionus* spp. (*B. angularis*, *B. calciflorus*, *B. quadridentatus*), *Asplanchna* sp., *Polyarthra* sp and *Filinia longiseta* additionally the biomass of *Anureopsis fissa*, *Notholca* sp., *Lecane* spp., *Pompolyx* sp., *Hexarthra* sp, *Trichocerca* sp., *Testudinella* sp., were also identified but the biomass were <1% of total rotifer during the study period. Furthermore, the contribution of rotifers to the total zooplankton biomass was very low (Fig. 5.24). Rotifer biomass was observed high in 2003, 2005, 2009 and 2010. Chl a concentration was positively correlated with rotifera biomass ($p<0.05$) particularly in 2005 the Chl a concentration reached 69.7±2.9 µg L^{-1}.

Throughout the study period *Keratella* displayed seasonal variation with two peaks in April and November. However, *Asplanchna* reached highest biomass on March. *Brachionus* and *Hexarthra* were reached the highest biomass during summer and after mid-summer *Polyarthra* appeared in lake.

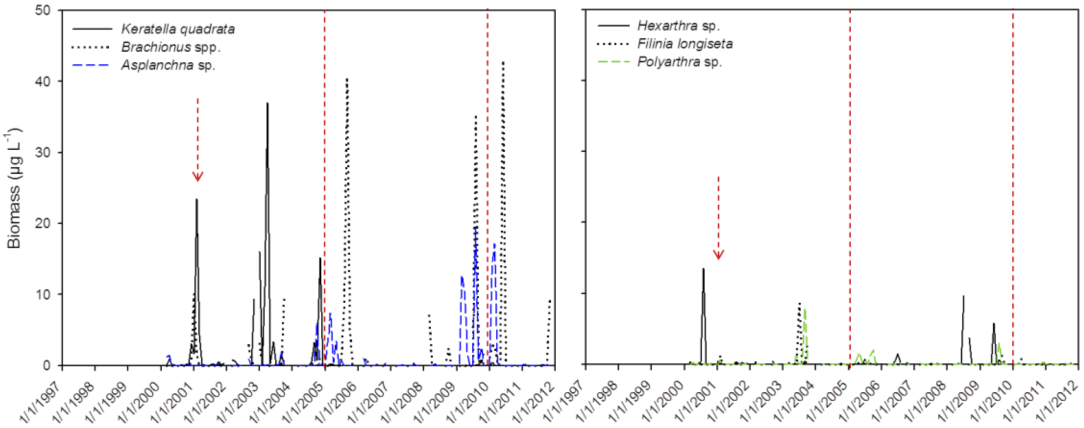

Figure 5.24. Biomass of Rotifer species in Lake Eymir from 2000 to 2012. Intervals of red dash line and arrow indicated the low water level periods.

The contribution of total zooplankton was mostly consisted of copepods from 1997 till 2005 since then the community composition shift to cladocerans during the low water level with high salinity and the period of second biomanipulation (Fig. 5.25).

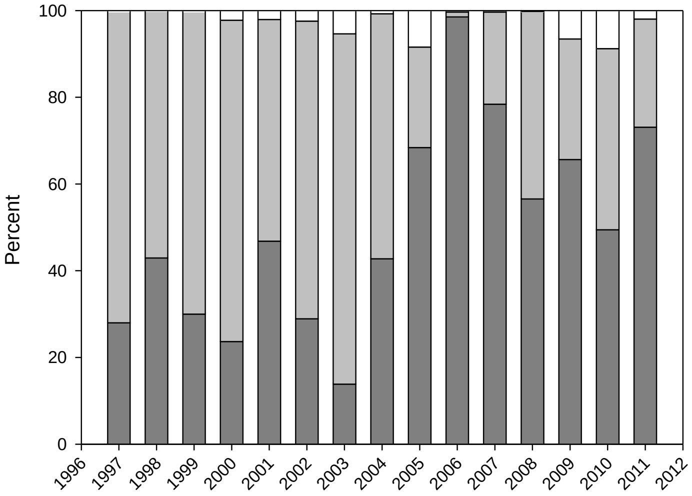

Figure 5.25. Percent of zooplanton groups in lake Eymir from 1997 to 2011. Dark grey: Cladocerans, light grey: Copepods and white: Rotifers. Note that no rotifer data in 1997, 1998 and 1999.

5.4. Discussion

The Lakes Mogan and Eymir received different impacts throughout of the study period (Fig. 5.26). The 15 years of dataset elucidated that there were two low water periods with high salinity including 2001 and period of 2005 to 2009; and high water level periods for the rest of the years in both lakes. Furthermore, Lake Eymir had two biomanipulations first from 1998-1999 and the second has been started in 2006 and still continued.

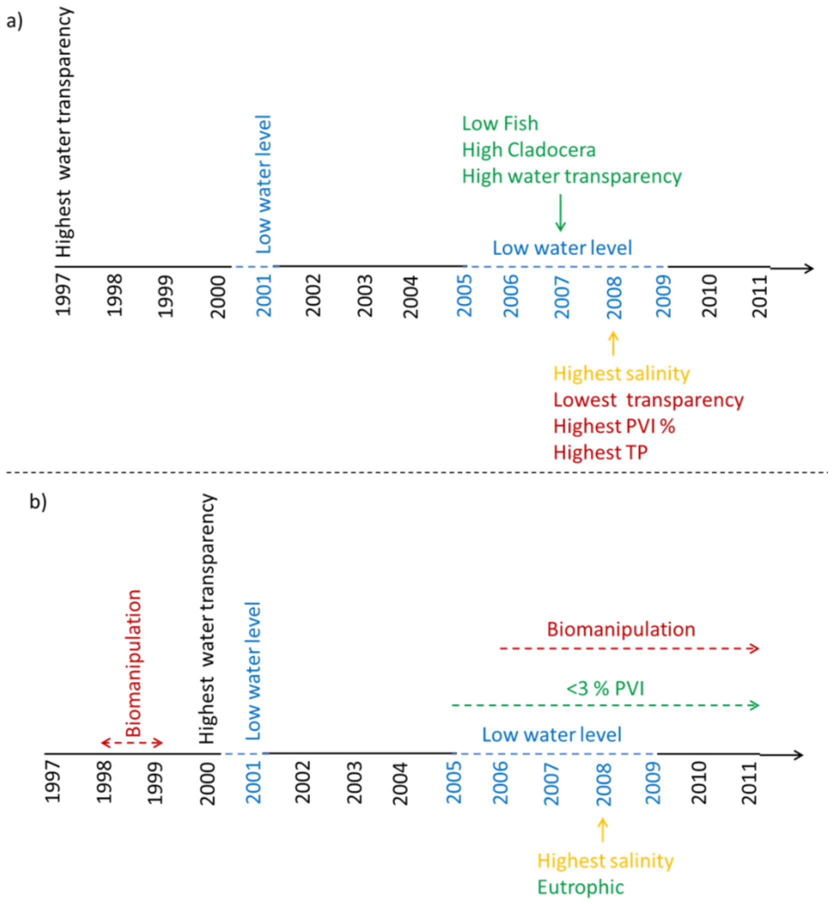

Figure 5.26. Chronology that shows the perturbations occurred in Lakes a) Mogan b) Eymir

In both lakes the drop in water level triggered large increase in salinity concurrently exacerbated the eutrophication via internal processes though lower the water quality. In addition, biomanipulation of downstream Lake Eymir created major differences in fish predation between lakes. Thus, removal of plankti-omnivorous fish, which is one of the widely used restoration processes for eutrophic lakes, (Meijer et al., 1999; Søndergaard et al., 2000) reduced the top-down control on zooplankton in lake.

In Lake Mogan, the main observed disturbance throughout the year was water level drop induced salinity and eutrophication. The prominent increase in salinity and decrease in water quality during low water level period influence the zooplankton community composition. In 1997 the lake was at clear water state with high transparency with low chlorophyll *a* and nutrient concentration onward the water clarity decreased gradually (Burnak & Beklioğlu 2000). Zooplankton community composition was mostly dominated by copepods and large sized *Daphnia longispina*. The high water transparency between 1997 and 2000 decreased with the drop in water level in 2001. Fish predation may have been high during these years because the zooplankton community consisted of small-medium sized cladocerans (e.g. *Ceriodaphnia*) and calanoid copepods *A. bacillifer* which have evasive skill against predator (O'Brain, 1979). Furthermore, during high salinity with low water period, submerged plant coverage consisting of mostly *Potemogeton* which is a cosmopolite species (Wiegleb & Kaplan, 1998; Vári, 2012) that can tolerate salinity (Wijck et al., 1994) reached to 60% with a simultaneous decrease in chlorophyll *a* and TP concentrations. This observation concurred with the general tendency that the drop in water level or low water levels can trigger the development of submerged macrophyte in non-eutrophic lakes (Havens et al., 2004; Beklioğlu et al., 2006). Moreover, low water level can override the effects of nutrient and fish predation and allowed submerged plant grow and expanded in contrast to northern lakes as observed in a mesocosms experiment, which simulated water level and fish predation, carried out in Lake Eymir (Bucak et al., 2012).

With the decrease in water level onward 2004, salinity increased 2 fold, similarly, the biomass of grazer *Daphnia magna* which is less vulnerable to high salinity. Furthermore, in-lake TP concentration was also very high as a result of internal processes instead of external loading (Özen et al., 2010).

Thus eutrophicated with anoxic conditions and frequent fish kills, which was reported from local newspaper (Anonymous, 2007; Anonymous, 2009), allow large sized predation sensitive but salinity tolerant *D. magna* became dominant. As observed in previous water level drop, which was occurred only one year, the coverage of submerged macrophyte consisting of saline tolerant *Potemogeton pectinatus* and *Najas marina* increased however did not promote clear water during this second period of water level drop which had been hold for five years.

Throughout the study period zooplankton community was dominated by calanoid copepod *A. bacillifer* which did not accord with any changes in physical and chemical conditions. However *D. longispina,* which was confirmed as sensitive to salinity stress (Gonçalves et al., 2007), was found significantly higher during low salinity with high water level periods. On the other hand, besides *Asplanchna*, biomass of the other rotifer species (*Filinia*, *Brachionus*, *Keratella*, *Hexarthra* etc.) did not have a high contribution throughout the study period. Moreover, despite the biomass of *Filinia* and *Brachionus* was low, their biomass significantly increased during high salinity with low water level period.

However, in Lake Eymir, water level fluctuation and biomanipulation have important consequences on the aquatic environment. There were two biomanipulation periods covering both low and high water levels. First biomanipulation was performed during high water level period with low salinity. Before and during the first biomanipulation period, water quality of the lake was poor and lake was dominated by large sized cyprinids which were responsible for turbidity through stirring up the sediment (Beklioğlu et al. 2003; Meijer et al. 1999).

Furthermore, zooplankton community composition was mostly dominated by calanoid *Arctodiaptomus bacillifer*, which had high evasive skill at high predation and small sized *Ceriodaphnia* sp. (autumn peak) as expected from size efficiency hypothesis (Brooks & Dodson, 1965). Onward 50% of cyprinid fish removal, lower the top down control on large sized *Daphnia pulex* thus the water clarity improved (Beklioğlu et al., 2003). However, clear water state was not long-lasting because of the water level drop and increased hydrologic stress; act as catastrophic disturbance which resulted in increased salinity and high nutrient concentration in 2001.

However, large sized *Daphnia pulex* still existed in high biomass despite the salinity reached 1.2‰. Bezirci et al. (2012) stated that 0.80-1.50 g L^{-1} of salt caused decreases in *D. pulex* survival and at >2‰ level of salinity *Daphnia* disappeared in Danish lakes (Jeppesen et al., 2005). Thus, *D.* pulex was able to tolerate 1.2‰ salinity concentration in Lake Eymir. On the other hand, due to the relatively high density of the fish, *Daphnia* displayed diel vertical migration to avoid fish predation supporting previous study (Muluk & Beklioğlu, 2005; Tavşanoğlu et al., unpubl. data). Although the submerged plant cover was ca. 50 % PVI during relatively high saline and low water level in 2001, it did not maintain the clear water state initiated by the first biomanipulation. Furthermore, observed plant species were cosmopolite and were able tolerate salinity. Thus, concurring with the previous studies for warmer lakes, in Lake Eymir also, submerged plants had no positive effect on clarity (Bachmann et al., 2002; Meerhoff et al., 2007b; Bucak et al., 2012). Subsequent years, salinity concentration decreased with the increasing water level. In addition, the tench and carp biomass reached the same level as the pre-biomanipulation period meanwhile pike was not recorded since 2003. Meanwhile, zooplankton community composition mostly dominated by calanoid copepods; however the biomass of rotifer species *Keratella* and *Brachionus* increased. Particularly in 2005 *Brachionus* which was known as the indicator of eutrophic conditions displayed a peak.

Second fish removal started in 2006 and triggered sudden improvement in the lake water quality. Due to a major reduced fish predation, *Daphnia magna* appeared in the lake with high biomass and chlorophyll a concentration decreased due to the possible increase in grazing pressure (Daphnia:Chla=40). However, the clear water conditions was not last long as progressive increase in water level deteriorated the water quality despite continuing biomanipulation. In comparison to the previous decrease in water level (2001), the water level drop during the period of 2005 to 2009, was extremely high particularly in 2008, concurrent ca. 2 fold increase in lake salinity. Furthermore, the lake was eutrophicated through up concentration of in-lake TP, DIN and TN with large contribution of ammonium mostly depended on internal processes rather than external loading as there was no inflows to the lakes during low water level years (Özen et al., 2010).

Thus higher nutrient concentration destabilized the clear state in Lake Eymir. During this period fish assemblages were consisted of bleak, small carp and invasive top mount gudgeon as well as large carp and tench.

However ongoing biomanipulation reduced the top-down control on zooplankton thus allowed large sized *Daphnia magna,* which was also tolerant of saline conditions increased especially with the spring peaks. Hence *Daphnia magna* may have also undergone diel vertical migration to avoid predation which was confirmed both laboratory (Tavşanoğlu et al., 2012) and field experiments (Tavşanoğlu et al., unpubl data) for Lake Eymir. Moreover, medium sized *Diaphanasoma* which was recorded up to 30‰ salinity level in several lagoons (Ustaoğlu et al., 2012); they were also coexisted with *D. magna* up to 10‰ salinity (Ustaoğlu et al., 2012) during mid-autumn. Calanoid copepods are typical zooplankton group for eutrophic brackish systems (Jeppesen et al., 2004; Brucet et al., 2009). Our results were also consistent with the literature that calanoid copepod *A. bacillifer* was observed high biomass in lake. Afterwards with increasing water level after 2010, water transparency improve ca. 2 fold concurrently the nutrient level decreased. Moreover, 70% of the total zooplankton biomass was consisted of cladocerans.

In lakes, dominancy of calanoid copepods which did not exhibit significant difference between periods is an indicator of intense fish predation. However under slight predation pressure, large sized *Daphnia magna* exist thus this may be the reason of developing an effective anti-predator response such as vertical migration or turbidity may serve as refuge against visual predators. In addition, both lakes were consisted of similar rotifer species at high predation periods which can tolerate changes in salinity. Although rotifers were globally diverse with >2000 species (Segers, 2007), few species can tolerate salinity changes (Fontaneto et al., 2006).Thus, rotifer abundance mostly determined by salinity (Kaya et. al., 2010). Furthermore, salinity affects the survival; abundance and reproduction (Williams, 1987; Schuytema et al., 1997) of zooplankton through influencing trophic interactions.

This is the first study elucidating the changes in the zooplankton groups and influencing factors by using long term monitoring data from Turkey. Throughout the study period both Lake Mogan and biomanipulated Lake Eymir experienced hydrological changes. On the other hand, despite biomanipulation had positive effect on the water quality by reducing top down control on zooplankton, hydrological changes override the impact via enhanced nutrient level.

Meanwhile, even if high submerged macrophyte presence low water level with high salinity did not lead the clear conditions. Thus present study suggested that water level fluctuation induced salinity and eutrophication with fish kill have strong impact on the trophic interactions in semi-arid Mediterranean region.

CHAPTER 6

CONCLUSION

The current study covering experimental and field work as well as long term monitoring data has confirmed that zooplankton community composition is strongly controlled primarily by fish predation but also by salinity.

The results suggest that eutrophication has a strong influence on the zooplankton community via fish predation and nutrient loading in Turkish lakes. Therefore particularly small fish are negatively related to the size diversity. Furthermore, increased fish density influence the community size structure of zooplankton towards small size in lakes located in lower latitudes. Moreover, small fish aggregate among submerged plants, thereby submerged plants may not provide day time refuge for zooplankton against fish predation. On the other hand, salinity might play an important role by decreasing species richness as well as biomass of zooplankton. Thus, the excessive usage of lakes as well as ongoing warming entail lakes becoming more eutrophic. This example from Turkish lakes may be an implication for the Mediterranean region (Chapter 2).

We found clear evidence from the field study with artificial plant systems that submerged macrophytes do not serve as a refuge for zooplankton in Turkish shallow lakes owing to the dominant fish communities, mostly composed of cyprinids, that are significantly associated with plants. Thus, our results imply that diel vertical migration of zooplankton, including rotifers as well as large sized species, are the most frequent predator avoidance strategy. The results of our study suggest that size structure and the distribution pattern of zooplankton may be controlled by fish predation and the use of submerged plant as a refuge may be weak in Mediterranean shallow lakes which may adversely influence the water transparency. Furthermore, the investigation of zooplankton migration pattern and size structure mostly depend on the visual/tactile predator. Accordingly, smaller individuals were not as vulnerable as larger ones against predation. Thus small size is an indicator of predation pressure in lakes (Chapter 3).

The laboratory experiment performed with cues obtained from fish and *Daphnia* conspecifics showed that *Daphnia magna* did not use plant as a refuge under the predation risk, instead prefering to reside within the sediment. The effect did not change with the water level changes (Chapter 4). These laboratory findings strongly support the field observations given in Chapter 3.

According to the 15 years of data from 1997 to 2011, the first extensive dataset from Turkey, the two interconnected shallow Lake Mogan and biomanipulated Lake Eymir experienced both low and high water level periods (Chapter 5). A drop in water levels triggered salinity and eutrophication in lakes. Despite the eutrophic condition prevailing in lakes during the low water level period, large sized *Daphnia* spp., especially salt tolerant *Daphnia magna*, predominated. Induced fish kill as a result of severe anoxic condition in lakes and further biomanipulation practices in Lake Eymir reduced the top-down control on large bodied *Daphnia*. Thus, large bodied individuals may survive by developing an effective anti-predator response such as vertical migration; furthermore, turbidity creates a refuge against visual predator.

In this thesis four different study approaches were used: Laboratory experiments, *in-situ* mesocosm experiments, snap-shot sampling and long term monitoring. The combination of these four approaches indicate that the zooplankton community composition is controlled by both top-down and bottom-up forces (Fig. 6.1.).

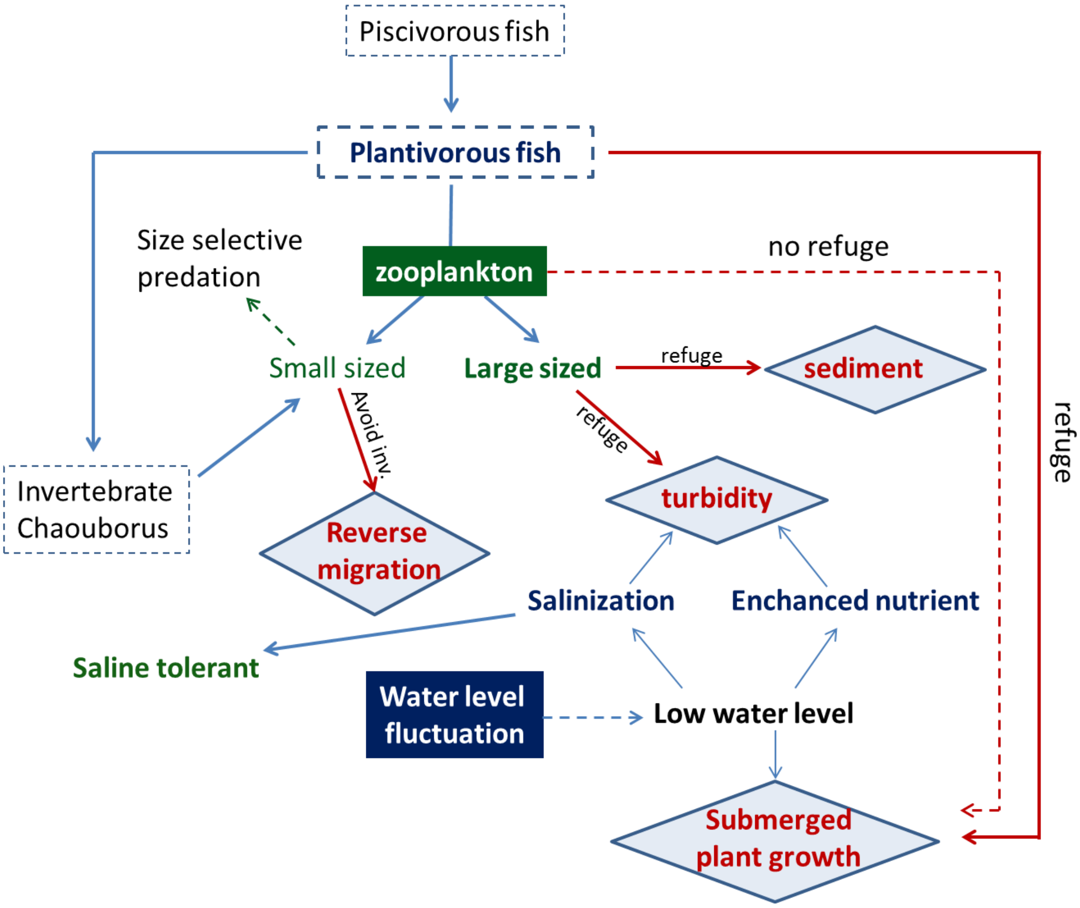

Figure 6.1. Schematic description of factors influencing trophic cascade with special focus on zooplankton.

In sampled shallow lakes, fish assemblages were mostly dominated by Cyprinids that prefer to aggregate among submerged plants. Through size selective predation small sized individuals have an advantage over large bodied individuals. However, large bodied individuals also exist in lakes by developing anti-predator behavior such as diel vertical migration. Due to the aggregation of fish among plants, sediment serves as an alternative refuge for zooplankton.

On the other hand, the semi-arid Mediterranean region lakes often experience water level fluctuations. Thus induced salinity and nutrient enrichment influence the trophic interactions.

A drop in water level promotes submerged plant development. However, high plant coverage did not lead to clear water in lakes.

Furthermore, lakes were commonly eutrophic and turbidity may serve as a refuge for zooplankton against visual hunting predators. However, zooplankton underwent reverse vertical migration against tactile predators (e.g. *Chaoborus* sp.).

Moreover, increased salinity concentration in lakes caused the existence of saline tolerant and high escape ability zooplankton species. The removal of fish can also lead to clear water due to reduced top down control on zooplankton; however, decrease in the water level may override the impact as a result of increased concentration in lake nutrient level.

Finally, when considering the influencing factors on zooplankton community, not only top down but also the direct effects of water level fluctuation should be included for Turkish shallow lakes. Otherwise the management practices will be frustrating.

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APPENDIX A

The locality of sampled lakes

No	Lake Name	Locality	Coordinates (N;E)		Area	Depth
1	Hamam	Kırklareli	41,82333	27,96560	20	1,6
2	Pedina	Kırklareli	41,83020	27,93421	10	0,55
3	Saka	Kırklareli	41,80278	27,99342	5	2,5
4	B. Akgol	Sakarya	41,04766	30,56439	190	3,7
5	Buyuk	Yedigöller	40,94388	31,74607	2,4	15,2
6	Derin	Yedigöller	40,94298	31,74983	1,5	9,6
7	Nazli	Yedigöller	40,93894	31,74222	1,6	5,4
8	Ince	Yedigöller	40,93961	31,74086	0,1	1
9	Serin	Yedigöller	40,94592	31,74739	0,17	1,5
10	Taskisigi	Sakarya	40,87386	30,40078	90	3,4
11	K. Akgol	Sakarya	40,87856	30,43206	20	0,95
12	Poyrazlar	Sakarya	40,84244	30,47008	60	4,9
13	Yenicaga	Bolu	40,77969	32,02822	400	4,4
14	Gölcük	Bolu	40,65503	31,62741	4,5	5,2
15	Abant	Bolu	40,60757	31,28195	128	17,4
16	Cubuk	Bolu	40,48108	30,83481	20	5,6
17	Eymir	Ankara	39,82697	32,83269	125	3,2
18	Mogan	Gölbaşı	39,76908	32,79088	635	3
19	Gölcük	Simav	39,16903	29,08391	70	3,4
20	Emre	Afyon	39,10825	30,43783	25	4,3
21	GokGol	Konya	39,01052	32,83822	50	1,1
22	Karagol	İzmir	38,55797	27,21808	20	4,1
23	Golcuk	Ödemiş-	38,31069	28,02853	75	3,7
24	Yayla	Denizli	38,03118	28,46350	70	2
25	Gebekirse	Selçuk	37,98533	27,30431	75	5,4
26	Akgöl	Selçuk	37,99164	27,31889	75	2,5
27	Karagol	Denizli	37,73513	29,49533	2	4,7
28	Azap	Aydın	37,58702	27,44345	250	1,5
29	Sakli	Denizli	37,46644	29,23865	0,75	7,5
30	Golhisar	Burdur	37,11389	29,60628	400	1,6
31	Baldimaz	Dalaman	36,41725	28,50063	10	1,5

APPENDIX B

List of species found in the studied lakes. For Numbers see Appendix A.

Taxa	Localities
CLADOCERA	
Acroperus angustatus Sars, 1863	12
Acroperus harpae (Baird, 1835)	15
Alona sp.	21
Alona guttata Sars, 1862	5,7,8
Alona quadrangularis (O.F. Müller, 1785)	12,22
Alona rectangula Sars, 1862	11,3,23,21,19
Alonella exigua (Lilljeborg, 1853)	15,24,29
Bosmina longirostris (O.F. Müller, 1785)	12,5,7,8,11,4,16,14,30,22,23,20,19, 25
Ceriodaphnia dubia Richard, 1894	15
Ceriodaphnia laticaudata P.E.Müller, 1867	4,27
Ceriodaphnia megops Sars, 1862	1
Ceriodaphnia pulchella Sars, 1862	30
Ceriodaphnia quadrangula (O.F. Müller, 1785)	1, 4,5, 12,14,20,29,30
Ceriodaphnia sp.	9,10,13,30,3,25,21,22
Chydorus spharicus (O.F. Müller, 1776)	5,8,9,10,11,12,15,16, 20,21,24,25,27,28
Daphnia galeata Sars, 1864	22,23
*Daphnia longispin*a O.F. Müller, 1875	5
Daphnia magna (Straus, 1820)	17,14
Daphnia pulex Leydig, 1860	30
Daphnia spp.	5,10,12,13,14, 19,22,23,20,21,27,28, 29,30
Diaphanosoma brachyurum (Lievin, 1848)	1,3, 4,10,14,17,30
Diaphanosoma sp.	4,12,15,18
Diaphonosoma mongolionum Ueno, 1938	23
Ilyocryptus spp.	3,19
Leydigia leydigi (Schoedler, 1863)	26,3
Macrothrix sp.	21,28
Moina branchiata (Jurine, 1820)	3,28
Moina macrocopora (Straus, 1820)	1,11,21
Moina micrura Kurz, 1874	4,11
Moina spp.	3,5,23,30
Pleuroxus aduncus (Jurine, 1820)	21

Pleuroxus uncinatus Baird, 1850	13,21
Pleuruxus truncatus (O.F:Müller, 1785)	15
Pleuroxus sp.	12
Polyphemus pediculus (Linnaeus, 1761)	15
Simocephalus vetulus (O.F. Müller, 1776)	5,21
COPEPODA	
Arctodiaptomus bacilifer (Koelbel, 1885)	16, 17
Cln. Copepod	1,3,12,13,14,15,22,24, ,25,26,28,29,30
Cyc. copepod	1,2,3,5,6,7,8,9,10,11, ,12,13,14,15,16,17, 19,20,22,23,24,25,26,27,28,29,30
ROTIFERA	
Anureopsis fissa Gosse, 1851	1,2,3,12,6,8,17,18,19,20,21,23,24,27,28,29, 31
Ascomorpha ecaudis Petry, 1850	7,12,16,31
Ascomorpha sp.	14,29
Asplanchna brightwelli (Gosse, 1850)	3
Asplanchna pridonta Gosse, 1850	6
Asplanchna spp.	1,3,5,6,7,8,9,12,13,16,19,20,21,22, 23,24,27,28,29,30
Brachianus falcatus Zacharias, 1898	1,3,25
Brachionus angularis Gosse, 1851	1,2,3,6,7,9,17,19,20,21,22,24,27,28,29,30,31
Brachionus bidentatus Anderson, 1889	2
Brachionus budapestinensis Daday, 1885	28
Brachionus calyciflorus Palas, 1766	3,6,9,11,17,21,22,23,26,28
Brachionus diversicornis (Daday, 1883)	4,10,11,16,18,22,23
Brachionus patulus (O.F. Müller, 1786)	2,4
Brachionus plicatilis (O.F. Müller,1786)	18,20,25,31
Brachionus quadridentatus Hermann, 1783	3,10,17,20,27,30
Brachionus rubens Ehrenberg, 1783	26
Brachionus spp.	3,6,12,18,21
Brachionus urceolaris (O.F. Müller, 1773	28
Cephalodella sp.	5,18,23,27
Colurella adriatica Ehrenberg, 1831	2,3,7,9,19,21,27
Colurella obtusa (Gosse, 1886)	5,12,15,19,21,27,28

Colurella uncinata (O.F. Müller, 1773)	5,9
Colurella sp.	8
Conochillus hippocrepis (Schrank, 1830)	15
Conochillus sp.	2,4
Euclanis dilatata Ehrenberg, 1832	12,15
Euclanis incisa Carlin, 1939	3,27
Euclanis sp.	18
Filina terminalis (Plate, 1886)	17
Filinia longiseta (Ehrenberg, 1834)	1,3,8,10,11,12,15,16,17,18,25,26,30 20,21,23,28
Filinia opoliensis (Zacharias, 1898)	1,12,15
Gastropus spp.	2,28
Hexarthra intermedia (Wiszniewski, 1929)	5,24
Hexarthra mira (Hudson, 1871)	10
Hexarthra spp.	1,2,3,10,11,12,13,16,18, 20,21,24,25,26, 27,28,29,30
Keratela tropica (Apstein, 1907)	4,6,21,22,23,28
Keratella cochlearis (Gosse, 1851)	1,3,4,5,6,7,8,9,10,11,12,14,16,19,20, 22,23,27,30
Keratella quadrata (O.F. Müller, 1786)	13,17,18,19,26,27,29,30
Keratella tecta (Gosse, 1851)	3,12
Lepadella patella (O.F.Müller, 1786)	5,9,12,15
Lepadella quadricarinata (Stenroos, 1898)	8
Lapedella spp.	2,12,16,18,19,21,24,27
Lecane spp.	1,2,3,4,5,8,12,15,16,17,18,19,21,24,27,28,29
Mytilinia sp.	8,24
Notholca acuminata (Ehrenberg, 1832)	8
Notholca sp.	30
Platyias quadricornis (Ehrenberg, 1832)	2,21
Polyarthra dolycoptera Idelson, 1925	4,7
Polyarthra major Buckhardt, 1900	9,12
Polyarthra remata (Skorikov, 1896)	16
Polyarthra spp.	1,2,3,4,7,9,11,12, ,14,15,16,18,19, 20, 21,23,24,25,27,28,29,30
Pompholyx sulcata Hudson, 1885	1,19

Rotaria sp.	17,18
Synchaeta sp.	15
Testudinella sp.	3,5,16,17,18,27,29
Trichocerca spp.	1,2,3,5,11,12,15,17,18,21,22,23,24,27,28,29,31
Trichocerca cylindrica (Imhof, 1891)	10
Trichocerca elongata (Gosse, 1886)	23
Trichocerca longiseta (Schrank, 1802)	1,4,10
Trichocerca pusilla (Lauterborn, 1898)	20,22,23,,29
Trichocerca rattus (O.F. Müller, 1776)	12,3,25
Trichocerca similis (Wierzeski, 1893)	1,3,4,9,12,18,19,20,23
Trichotria sp.	15,21,27

APPENDIX C

List of fish species in studied lakes. For Numbers see Appendix A.

TAXA	
CYPRINIDAE	
Abramis brama (Linnaeus, 1758)	4,10,11
Alburnoides bipunctatus (Bloch, 1782)	2,15
Alburnus demiri Özuluğ&Freyhof, 2008	25,26
Alburnus escherichi Steindachner, 1897	18
Alburnus orontis Sauvage, 1882	16
Alburnus spp.	1,3,11,13,17,18,28
Aspius aspius (Linnaeus, 1758)	3
Barbus sp.	13,15
Blicca bjoerkna (Linnaeus, 1758)	12
Carassius auratus (Linnaeus, 1758)	20
Carassius carassius (Linnaeus, 1758)	2,23
Carassius gibelio (Bloch, 1782)	19,28
Carassius spp.	1,2,3,21,22,29,31
Cobitis simplicispinna Hanko, 1925	4,19
Cobitis taenia Linnaeus, 1758	3,20,26,31
Cobitis sp.	18,28
Cyprinus carpio Linnaeus, 1758	2,3,4,13,16,17,18,19,20,21,26,27,29
Esox lucius Linnaeus, 1758	4,12
Gobio gobio (Linnaeus, 1758)	2,13
Leuciscus cephalus (Linnaeus, 1758)	5,7,8,9,13,14,24,30
Petroleuciscus smyrnaeus (Boulenger, 1898)	22,26
Pseudophoxinus sp.	19
Pseudorasbora parva (Temminck & Schlegel, 1846)	17,18,28
Rhodeus amarus (Bloch,1782)	3
Rhodeus sp.	1,12
Rutilus rutilus (Linnaeus, 1758)	12,23
Scardinius erythrophthalmus (Linnaeus, 1758)	1,2,3,4,10,11,12
Tinca tinca (Linnaeus, 1758)	4,5,9,12,13,14,15,16,17,18,30
Vimba vimba (Linnaeus, 1758)	3

List of fish species in studied lakes (continued).

TAXA	
ATHERINIDAE	
Atherina boyeri Risso, 1810	1,4,10,12,25,26,31
MUGILLIDAE	
Liza sp.	28
Mugil cephalus Linnaeus, 1758	25,26
PERCIDAE	
Perca fluviatilis Linnaeus, 1758	10,11,12
Stizostedion lucioperca (Linnaeus, 1758)	1,25,30
SALMONIDAE	
Oncorhynchus mykiss (Walbaum, 1792)	5,6,7,8,9,
Salmo trutta Linnaeus, 1758	5,6,7,9,15
BALITORIDAE	
Nemacheilus lendli (Hankò,1925)	19
CENTRARCHIDAE	
Lepomis gibbosus (Linnaeus, 1758)	3,28
CICHLIDAE	
Tilapia sp.	31

APPENDIX D

Mean±SD of variables in Lake Mogan and Eymir from 1997 to 2011 during high and low water level periods.

	EYMİR		MOGAN	
	HWL	**LWL**	**HWL**	**LWL**
Secchi-depth (cm)	217.8±138.2	176.9±119.3	157.78±78.4	117.33±88.5
SS(mg/l)	12.3±16.6	14.8±11.1	11.27±7.61	19.2±14.3
Chl a (µg/l)	21.2±26.3	30.8±52.6	13.63±12.71	13.07±10.6
TP (µg/l)	266.9±162.1	301.0±132.0	87.46±43.32	88.26±41.5
SRP (µg/l)	168.8±153.1	202.9±152.7	22.17±21.14	32.96±19.9
nitrate+ nitrite (µg/l)	145.8±147.9	251.4±202.8	135.42±154.78	137.8±131.5
Ammo-nium (µg/l)	222.3±280.1	314.4±316.7	188.44±297.79	121.7±133.5
DIN (µg/l)	342.2±326.0	563.1±411.1	292.10±371.76	259.5±233.6
TN (µg/l)	1522.9±938.2	2770.3±1395.6	1421.23±1004.66	1492.80±483.3
Conduc-tivity (mS)	2.2±0.4	2.8±0.5	2.48±0.47	3.57±0.81
TDS (g/l)	1.3±0.3	1.6±0.5	1.43±0.40	2.06±0.7
Salinity ‰	1.14±0.2	1.46±0.29	1.19±0.25	1.85±0.5

CURRICULUM VITAE

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TUBİTAK-ÇAYDAG 110Y125,

Project Manager: Prof. Dr. Meryem Beklioğlu.

"Adaptive strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems"

EU- FP7 proje no ***244121,***

Proje Coordinator : University College of London,

Project Partner: METU

“Adaptation to Climate Change and Protection of Biodiversity through Conserving and Sustainable Use of Wetlands in Turkey”. Deustche Gesellschaft Technise Zusammenarbeit (GTZ),

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“The Conservation Of Turkish Shallow Lakes By Determining The Interactions Between Their Ecological Structure, Climate And Anthropogenic Use With Holistic And Sensitive Methods And The Development Of Strategies For Their Restoration “

TUBITAK-CAYDAG-105Y332,

Project Manager: Assoc. Prof. Dr. Didem Oğuzkurt,

Researcher: Prof. Dr. Meryem Beklioğlu Yerli