Faculty of Biological and Environmental Sciences
Department of Environmental Sciences
University of Helsinki
Finland

THE ROLE OF ENVIRONMENTAL FACTORS IN REGULATING PLANKTIVOROUS PREDATION

INTERACTIVE EFFECTS OF TURBULENCE AND VISIBILITY CONDITIONS

Laura Härkönen

ACADEMIC DISSERTATION

To be presented, with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki, for public examination in Walter Auditorium, Agnes Sjöbergin katu 2, Helsinki, on August 1 2014, at 12 noon.

Helsinki 2014

Supervisor: Prof. Jukka Horppila
Aquatic Sciences
Department of Environmental Sciences
University of Helsinki
Finland

Reviewers: Prof. Christer Brönmark
Aquatic Ecology
Department of Biology
Lund University
Sweden

Dos. Anne-Mari Ventelä
Pyhäjärvi Institute
Finland

Opponent: Assoc. Prof. Mariana Meerhoff
CURE-Facultad de Ciencias
University of the Republic
Uruguay

Custodian: Prof. Hannu Lehtonen
Aquatic Sciences
Department of Environmental Sciences
University of Helsinki
Finland

ABSTRACT

Visibility conditions of lakes in the Northern Hemisphere have been predicted to decline, due to climate change- induced variations in vegetation of the surrounding catchment areas, precipitation, soil erosion, as well as sediment resuspension. At the same time, climate models predict increasing wind and storm activities, resulting in increasing turbulent velocities, especially within the mixed surface layer of lakes. Additionally, the decrease predicted in summertime cloudiness may lead to stronger warming of surface-water layers and thus enhanced turbulent velocities in lake ecosystems, due to intensifying nighttime convection. Hence, decreasing visibility conditions and, on the other hand, increasing turbulence conditions are both predictable changes in the abiotic environment of lakes.

The aim here was to experimentally clarify how these changes in abiotic factors may affect planktivorous predation in lake ecosystems. We aimed at clarifying how turbulence affects the ability of pelagic invertebrates (*Chaoborus flavicans*) to avoid fish predation by altering their distribution, the feeding efficiency of *C. flavicans* and planktivorous perch (*Perca fluviatilis*) under varying turbidity conditions, and the response of the zooplankton community to various predators, i.e. pelagic invertebrates (*Chaoborus*), and fish (perch and roach (*Rutilus rutilus*)) in highly colored water.

Increasing turbulence negatively affected the ability of *Chaoborus* larvae to exploit their vertical refuge and also to determine their horizontal position, which in turn was assumed to affect their predator escape efficiency. Indeed, a positive interaction of turbulence and turbidity with planktivorous perch feeding was discovered. Our novel findings challenged the previous assumption that fish larger than a few centimeters in body length are unaffected by turbulence. The proportion of chaoborids consumed under turbulent and turbid conditions showed a dome-shaped response, being highest with the dissipation rate of turbulent energy exceeding 10^{-5} m^2 s^{-3}. This was attributed to increased encounter rates between predators and prey, as well as difficulties of chaoborids in escaping predators under high turbulence; the time lost in searching for the prey was compensated. Additionally, intermediate turbulence (dissipation rate 10^{-6} m^2 s^{-3}) combined with humic water altered the selective feeding of planktivorous fish on zooplankton compared with under calm conditions. Under turbulent conditions, planktivorous fish preferred copepods over cladocerans, whereas under calm conditions the contrasting situation prevailed. Turbulence-mediated changes in the selective feeding of planktivorous fish under low visibility conditions may result in drastic changes in the lower trophic levels in fish-dominated systems.

The studies also revealed that intermediate turbulence (dissipation rate 10^{-6} m^2 s^{-3}) benefits the feeding of pelagic invertebrate predators, such as *Chaoborus flavicans*, but only when introduced to a natural, versatile zooplankton community. In contrast to the effect of fish predation, the dark-water experiments in mesocosms showed that the combined effect of turbulence and *Chaoborus* predation was

strongest on cladocerans. In lakes, cladocerans are some of the most important consumers of phytoplankton; in circumstances dominated by *Chaoborus* larvae as invertebrate predators, a modest increase in turbulence can substantially influence herbivorous zooplankton. High turbulence (dissipation rate $\geq 10^{-5}\,\mathrm{m^2\,s^{-3}}$), on the other hand, caused decreases in *Chaoborus* feeding, which was also attributed to difficulties of chaoborids in maintaining their horizontal position.

We suggest that turbulence together with varying visibility conditions can have crusial implications for planktivorous predation and should thus be treated as a significant factor in food web studies. Furthermore, intermediate turbulence together with contemporaneous increases in water color may possibly result in cascading effects on primary producers. Depending on the dominant planktivores present, these changes in abiotic factors can have significant consequences on the lower trophic levels, with possible implications for even cascading trophic interactions.

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, referred to in the text by their Roman numerals:

I   Joensuu, L., Z. Pekcan-Hekim, N. Hellén, and J. Horppila. 2013. Turbulence disturbs vertical refuge use by *Chaoborus flavicans* larvae and increases their horizontal dispersion. Freshw. Biol. 58: 1997-2006.

II   Pekcan-Hekim, Z., L. Joensuu, and J. Horppila. 2013. Predation by a visual planktivore perch (*Perca fluviatilis*) in a turbulent and turbid environment. Can. J. Fish. Aquat. Sci. 70: 854-859.

III   Härkönen, L., Z. Pekcan-Hekim, N. Hellén, and J. Horppila. 2014. Feeding efficiency of *Chaoborus flavicans* under turbulent conditions. Hydrobiologia 722: 9-17.

IV   Härkönen, L., Z. Pekcan-Hekim, N. Hellén, A. Ojala, and J. Horppila. Combined effects of turbulence and different predation regimes on zooplankton in high-colored water – implications of environmental change for lakes. Manuscript.

The original publications included in this thesis are reproduced by the kind permissions of © John Wiley & Sons (**I**), © 2008 Canadian Science Publishing (**II**), and © Springer Science + Business Media (**III**).

AUTHOR'S CONTRIBUTION TO THE PUBLICATIONS

I   Härkönen (neé Joensuu) was responsible for designing the experiments, collected most of the data, performed the data analysis, and was responsible for manuscript preparation.

II   Härkönen participated in designing the experiments, collected most of the data, and took part in data analysis and manuscript preparation.

III   Härkönen was responsible for designing the experiments, collected most of the data, performed the data analysis, and was responsible for manuscript preparation.

IV   The initial idea for the experiments came from Härkönen. She had the main responsibility for designing the experiments, collecting data, performing the data analysis, and preparing the manuscript.

ABBREVIATIONS

ANOVA	analysis of variance
ANOVAR	analysis of variance for repeated measurements
C	calm water
Chao	*Chaoborus*
Chl *a*	chlorophyll *a*
DO	dissolved oxygen
DOC	dissolved organic carbon
ε	dissipation rate of turbulent kinetic energy
E	exposure time
HSD	honestly significant difference
IPCC	Intergovernmental Panel on Climate Change
NTU	nephelometric turbidity unit
RDA	redundancy analysis
Re	Reynolds number
RMS	root-mean-square
S	search time
T	turbulent water
TN	total nitrogen
TP	total phosphorus
Turb	turbulence
TV	total variation

1 INTRODUCTION

One of the main shortcomings in understanding the response of aquatic ecosystems to disturbances is the lack of a framework blending together physics and biology (Osborn and Scotti 1996). The distribution and abundance of species within a particular environment are determined both by tolerance to physical conditions and by interactions with other organisms (e.g. Hutchinson 1961). Organisms are influenced both physiologically and behaviorally by abiotic factors that may consequently influence the outcome of biotic interactions (Dunson and Travis 1991).

The Intergovernmental Panel on Climate Change (IPCC 2001) stated that, lakes are particularly vulnerable to changes in climate parameters. Variations in air temperature, precipitation, and other meteorological components directly cause changes in hydrobiological regimes through evaporation, water balance and lake level, and thus the entire lake ecosystem. Climate change scenarios in aquatic ecosystems in the Northern Hemisphere predict rising water temperatures, nutrient concentrations, and variations in external nutrient loading (Mooij et al. 2005; George 2010). Climate models also predict increasing wind and storm activities (Giorgi et al. 2004), which may lead to increasing turbulent velocities, especially within the mixed surface layer of lakes. Additionally, predicted decrease in summertime cloudiness (Giorgi et al. 2004) may lead to stronger warming of surface-water layers in daytime and thus enhanced turbulent velocities in lake ecosystems, due to intensifying nighttime convection. Visibility conditions in lakes are degraded through increasing turbidity and water brownification, which are caused by erosion from the surrounding soils, accelerated sediment resuspension due to turbulence, and increase in external loading of dissolved organic carbon (DOC), due to increased terrestrial vegetation and precipitation (Horppila and Nurminen 2003; Hongve et al. 2004; Evans et al. 2005; Wrona et al. 2006; Granéli 2012). Consequently, lakes are under continuous processes of change.

The characteristics of lakes are determined by interacting abiotic and biotic factors. Both bottom-up (resources) as well as top-down (predation) forces simultaneously affect ecological communities (Brett and Goldman 1997) by regulating bacterioplankton, phytoplankton, as well as zooplankton populations (e.g. Thingstad and Lignell 1997; Peters et al. 2002; Karlsson et al. 2009; Nicolle et al. 2011). The relative importance of top-down and bottom-up regulation in a given community may vary with season, the structure of the food web, and species composition (e.g. Vanni and Finlay 1990; Steiner 2001). Additionally, physical factors, such as light availability and water mixing can modify the strength of bottom-up and top-down forces, due to their effects on primary productivity and predator-prey interactions (Steiner 2001; Utne-Palm 2002; Liljendahl-Nurminen et al. 2003, 2008; Karlsson et al. 2009).

The top-down effect of predators on the lower trophic levels is regarded as a significant factor in structuring communities in lake ecosystems (McQueen et al. 1986; Vanni et al. 1990). Several studies have shown the importance of fish in structuring plankton communities in lakes (Hrbáček et al. 1961; Brooks and Dodson

1965; Lampert 1987), and the hypothesis of cascading trophic interactions suggests that predators strongly affect freshwater phytoplankton community structure and productivity (Carpenter et al. 1985). However, the cascading effect of planktivorous fish and zooplankton on phytoplankton often circulates through invertebrate predators, thus modifying the impact and strength of the cascading interactions (Wissel and Benndorf 1998; Ramcharan et al. 2001; Liljendahl-Nurminen et al. 2003). Additionally, the complex trophic relationships can be interconnected in a cascade or by a network of links, so that a change in any one component can affect the other components (Carpenter and Kitchell, 1988; Pace et al. 1999; Steiner 2001; Horppila and Liljendahl-Nurminen 2005).

1.1 PHYSICAL FACTORS AND TOP-DOWN CONTROL IN LAKE ECOSYSTEMS

1.1.1 TURBULENCE

Turbulence is an increasingly studied abiotic factor that can affect both bottom-up and top-down control in aquatic ecosystems. Turbulence is the irregular, diffusive, dissipative flow of water without any preferred velocity direction (Tennekes and Lumley 1972). Most flows occurring in nature are turbulent, caused by flow instabilities related to the interaction of viscous and nonlinear inertial forces (Tennekes and Lumley 1972). In aquatic ecosystems, turbulence is caused by a variety of processes, including wind stress and buoyancy flux at the air-water interface, breaking internal waves in the interior, and drag at the water-sediment boundary (Imboden and Wüest 1995). In each case, turbulence is a key component in the cascade of energy from large scales (where energy enters the system) to small scales (where energy is dissipated due to viscosity). Additionally, it transports heat, momentum, and a variety of other tracers such as gases, nutrients, and organic material throughout the water column, thus affecting the physical and biogeochemical dynamics of lakes (Imboden and Wüest 1995).

Due to its high capacity for transferring constituents, turbulence has been denoted as a key driver in increasing predator-prey encounter rates (Rothschild and Osborn 1988; MacKenzie and Leggett 1991; Pecséli et al. 2010). Theoretical studies imply that small-scale turbulence enhances planktonic contact rates by increasing the relative motion between predators and prey (Rothschild and Osborn 1988). These findings suggest enhanced ingestion rates of zoo- and ichthyoplankton in turbulent environments (Marrasé et al. 1990; Sundby and Fossum 1990; MacKenzie and Leggett 1991). Ambush predators, such as phantom midge larvae (Diptera: Chaoboridae), are largely limited to attacks on prey entering their effective strike area, rather than actively pursuing their prey (Swift and Fedorenko 1975). Thus, the movement of prey is necessary for encounter and the interactions with potential prey are governed primarily by the distribution and swimming behavior of the prey. Consequently, increasing turbulence could play a significant role in the feeding rate of invertebrates by affecting the amount of prey items in their attack range. On the other hand, larger organisms, such as fish larger than a few centimeters in body

length, are assumed to be unaffected by turbulence due to their higher swimming speed (Kiørboe and Saiz 1995).

1.1.2 OPTICAL CONDITIONS

Light is a very important top-down regulator, due to its effects on the feeding efficiency of predators (Aksnes and Giske 1993). Depending on the light availability, dominance relationships between various predators may change drastically. The optical conditions in lakes are controlled by several mechanisms. Erosion from the surrounding soils or resuspension of the sediment causes turbidity of the water, due to suspended inorganic particles (Evans 1994; Horppila and Nurminen 2003; Lind 2003). Additionally, turbidity can be caused by organic particles, due to increased algal biomass in eutrophicated waters (Anderson et al. 2002). On the other hand, in boreal lakes, high DOC concentrations are frequent (Kortelainen 1993; Sobek et al. 2007) and numerous lakes are brown-watered with low visibility conditions. DOC is the main factor controlling water color in lakes (Pace and Cole 2002). Humic substances are mainly the products of decomposition of plant material, which is transported by surface runoff to lakes and streams from the surrounding catchment areas (Roulet and Moore 2006).

The foraging of visual predators may be weakened by reductions in water transparency and ambient light intensity (Vinyard and O'Brien 1976; Confer et al. 1978; Ranåker et al. 2012). Several studies have shown that degraded visibility negatively affects the reaction distances of fish (Gerritsen and Strickler 1977; Confer et al. 1978; Utne-Palm 2002) and consequently their feeding efficiency (Vinyard and O'Brien 1976; Horppila et al. 2004, 2011; Pekcan-Hekim and Lappalainen 2006). In turbid water, large particles such as clay, suspended sediment, or phytoplankton cells scatter incoming light, thus reducing the contrast between particles and their background (Kirk 1994; Utne-Palm 2002). The contrast between prey species and their backgrounds is one of the most important factors in prey detection by fish (Hinshaw 1985). The effects of turbidity and light availability on the feeding efficiency of particulate-feeding planktivorous fish have been demonstrated in several studies (Vinyard and O'Brien 1976; Horppila et al. 2004; Pekcan-Hekim and Lappalainen 2006). DOC, on the other hand, effectively absorbs light instead of scattering it (Kirk 1994), and in dystrophic lakes the contrast between particles and the background may be maintained at sufficient light levels. High values of water color may consequently be less damaging for fish feeding than ligh-scattering turbidity. Nevertheless, in contrast to clear-water lakes, humic substances absorb short wavelengths of light, resulting in a characteristic red light climate in dystrophic lakes (Eloranta 1978) with possible consequences for visual feeding. Indeed, there is evidence that fish growth rates (Rask et al. 1999; Horppila et al. 2010) as well as fish production (Karlsson et al. 2009) are affected by the level of DOC in the water.

Many invertebrate predators, on the other hand, do not rely on vision in detecting their prey and may predominate over planktivorous fish under low visibility conditions (Cuker 1993; Horppila and Liljendahl-Nurminen 2005). Since invertebrate predators are also important prey items for many planktivorous fish

species (Pope et al. 1973), they can coexist at high densities with fish only if they can find refuge against predation (Liljendahl-Nurminen et al. 2003). The risk of predation usually decreases with decreasing light levels. With planktivorous fish present, the highest densities of pelagic invertebrates are usually found in lakes with high turbidity levels (Liljendahl-Nurminen et al. 2003) or dark water color (Wissel et al. 2003). In structurally simple environments in the pelagic zones of lakes, low light intensities or high values of water color can provide refuge from visually oriented fish during daylight (Vinyard and O'Brien 1976; Lampert 1993). Consequently, many zooplankton species and pelagic invertebrates conduct diel vertical migrations between deep-water layers and the epilimnion (Lampert 1993; Lévesque et al. 2010). Additionally, predator avoidance regulates the horizontal movements of zooplankton towards the structural protection offered by vegetation in the littoral zone (Burks et al. 2002). However, in lakes where the littoral zone is narrow or low visibility conditions offer protection from fish predation, the importance of vegetation as a refuge is decreased (Snickars et al. 2004; Estlander et al. 2009).

1.1.3   INTERACTION OF TURBULENCE AND OPTICAL CONDITIONS

The interactive effects of turbulence and visibility conditions on planktivorous predation are poorly known. Since most fish are visual feeders, whereas many invertebrate predators are tactile predators, invertebrate predators may predominate over planktivorous fish under low visibility conditions (Cuker 1993; Horppila and Liljendahl-Nurminen 2005). Additionally, turbulence may affect mainly slowly swimming organisms, such as invertebrate predators (Eiane et al. 1997). Thus, the effects of turbulence on predation may also be dependent on visibility. Since tactile planktivores should profit most from turbulence, they could thus be capable of higher prey removal rates than planktivorous fish under low visibility conditions (Kiørboe and Saiz 1995; Eiane et al. 1997).

In addition to increasing encounter rates, turbulence can also disperse prey patches (Davis et al. 1991; Dower et al. 1997) and thus contribute to the determination of distributions of planktonic organisms. Consequently, turbulence may also affect the ability of zooplankton to avoid predation. In addition to predation risk and food abundance, abiotic factors such as currents can affect the horizontal distribution of zooplankton (Lévesque et al. 2010). Indeed, turbulence significantly affects the vertical dispersion of small, weak swimmers, such as ciliates and nauplii, and can disturb patch formation and vertical migration of crustacean zooplankton (Lagadeuc et al. 1997; Andersen et al. 2001; Maar et al. 2003). Turbulence can also exert a substantial effect on the escape responses of invertebrate prey (Lee et al. 2010). Additionally, there is evidence that turbulence may disperse *Chaoborus flavicans* Meigen larvae from their meta- and hypolimnetic refuges (Malinen et al. 2001).

Since both intermediate turbulence and low visibility should be more beneficial for tactile invertebrate predators than for fish (Kiørbie and Saiz 1995; Eiane et al. 1997), the predation effects on zooplanktonic prey populations combined with these abiotic factors could be considerably stronger in invertebrate-dominated systems

than in equivalent fish-dominated systems. If the assumption holds that planktivorous fish do not benefit from increasing turbulence, whereas invertebrate predators do, the planktivorous food web dynamics could be significantly affected. Moreover, the combined effects of low visibility and turbulence may lead to drastic changes in top-down control of lakes due to contradictory, yet unknown, responses of various predators to those abiotic factors.

Most fish have a well-developed visual system and use it as their primary source of information (Guthrie and Muntz 1993). Consequently, they generally feed on the largest, visually conspicuous prey, selecting mainly invertebrates, large cladocerans and copepods (Brooks and Dodson 1965; Wissel and Benndorf 1998). Intense planktivory by fish often results in a zooplankton community dominated by small species (Hrbáček et al. 1961; Brooks and Dodson 1965). Whereas fish are often visual feeders, many invertebrate predators, such as the pelagic chaoborids, cladocerans (e.g. *Leptodora kindti* Focke), and copepods, detect their prey by mechano- or chemoreception (e.g. Riessen et al. 1984; Browman et al. 1989; Yen and Strickler 1996; Fields and Yen 2002). In addition to fish, they are able to substantially affect the abundance of their prey and even the species composition of the community by feeding selectively among zooplankton (Allan 1973; von Ende 1979; Liljendahl-Nurminen et al. 2003). Invertebrate predators are often gape-limited and, in contrast to fish, usually select small- to medium-sized zooplankton (Pastorok 1981, Riessen et al. 1988). Consequently, the zooplankton communities subjected to heavy invertebrate predation are often dominated by large-bodied species (Zaret 1980). However, in many cases invertebrate predators occur simultaneously with fish. Due to their large size, invertebrates are conspicuous and thus also an important prey item for many planktivorous fish species (Pope et al. 1973). Co-occurrence with planktivorous fish often leads to intraguild predation in which the intraguild prey (invertebrate) is preyed upon by the top predator (fish) and to survive the intraguild prey must be more efficient in preying on the shared zooplankton than the fish (Holt and Polis 1997). The structure of the zooplankton community is thus often the result of a balance between fish and invertebrate predation. Due to their diverse feeding modalities, the two types of planktivores may have different effects on zooplankton communities. For the same reason, environmental factors may play a significant role in the feeding efficiencies of these divergent predators.

2 OBJECTIVES OF THE THESIS

The present study aimed at clarifying the effects of environmental factors in regulating vertebrate and invertebrate predation in aquatic ecosystems. The main objective of the thesis was to elucidate how changes in turbulence and light environment affect top-down control by pelagic planktivores.

The thesis is composed of four experimental studies aimed at clarifying how turbulence affects the ability of pelagic invertebrates (*Chaoborus flavicans*) to avoid fish predation by altering their distribution (**I**), the feeding efficiency of planktivorous fish (Eurasian perch (*Perca fluviatilis* L.)) under varying visibility conditions (**II**), the feeding efficiency of *C. flavicans* (**III**), and the response of the zooplankton community to various predators, i.e. invertebrates (*Chaoborus*) and fish (perch and roach (*Rutilus rutilus* (L.)) under turbulent conditions combined with low visibility (**IV**).

The thesis focuses on the following questions (Fig. 1):

1. Does turbulence affect the vertical and horizontal distribution of *Chaoborus* larvae (**I**)? Are there implications for planktivorous fish feeding under altered visibility conditions (**II**)?

2. Is the feeding efficiency of *Chaoborus* larvae affected by turbulence (**III**, **IV**)?

3. How do these different planktivorous predators (i.e. chaoborids and fish) affect the zooplankton community structure under turbulent conditions combined with low visibility (**IV**)?
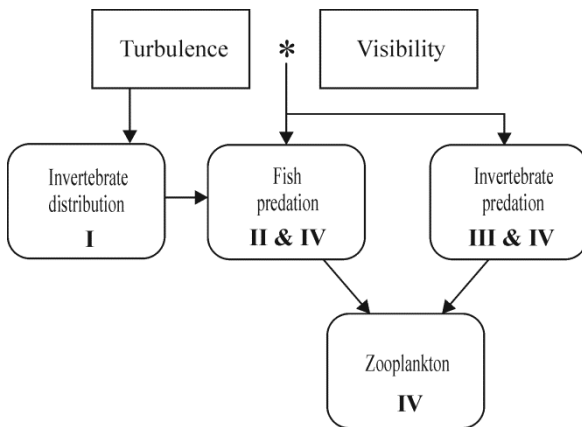

Fig. 1. Schematic summary of the organization of the study. The asterisk indicates the interactive effect of turbulence and visibility conditions.

3 MATERIALS AND METHODS

3.1 EXPERIMENTAL SETUPS

Laboratory experiments in aquaria were conducted to investigate the effect of different turbulence levels on the distribution (**I**) and feeding (**III**) of pelagic invertebrate predators (*C. flavicans*), and the combined effect of these levels together with altered turbidity conditions on planktivorous perch feeding (**II**). The interactive effect of turbulence and low visibility induced by high levels of water color on the predation effect of various predators on the zooplankton community structure was investigated with outdoor mesocosm experiments (**IV**).

3.1.1 AQUARIA IN LABORATORY EXPERIMENTS

Research on the effect of various turbulence levels on the vertical distribution of *C. flavicans* larvae was conducted in a vertical cylinder containing 46 L of tap water (**I**) and in the horizontal direction in an aquarium containing 200 L of tap water (**I**). To investigate the effect of turbulence on the distribution of chaoborids in both directions, their aggregation into predetermined locations had to be ensured. The larvae, being negatively phototactic (Teraguchi and Northcote 1966; Parma 1971; Gliwicz et al. 2000), were aggregated by providing them a darkened area (refuge) at either end of the aquarium or in the bottom layer of the cylinder by covering the areas with dark plastic. In the vertical setup, the refuge area covered 45% and in the horizontal setup 33% of the total water volume in the experimental unit. Control treatments under uniform darkness were performed in both directions.

Studies on the effects of increasing turbulence on the feeding efficiency of planktivorous fish were conducted in two acrylic aquaria containing 200 L of tap water including varying levels of inorganic turbidity (**II**). Two acrylic aquaria containing 100 L of tap water were used to investigate the effect of increasing turbulence on the feeding efficiency of *C. flavicans* larvae (**III**).

3.1.2 OUTDOOR PONDS IN MESOCOSM EXPERIMENTS

Mesocosm studies were conducted during the summer of 2012 in outdoor ponds (area 8.1 m^2, volume 3200 L) in the Evo district (61°13'N, 25°12'E), southern Finland (Fig. 2).

Fig. 2. Outdoor mesocosms used and a schematic presentation of one pond (**IV**). Three complexes including 12 ponds were employed in the experiments (one complex shown in the figure) using eight identical ponds in the middle of each complex, leading to a total number of 24 ponds. The wavy dashed line in the schematic presentation indicates the water table; the single arrows represent water inlets and the splitting arrows water outlets of the pumps.

The maximum depth of the ponds was 60 cm, with an average depth of 40 cm. The ponds had a sand-gravel bottom (grain size 0.1–2 cm) with a 0.5–1-cm layer of organic debris with no vegetation (**IV**).

3.2   ENVIRONMENTAL CONDITIONS

3.2.1   VISIBILITY CONDITIONS IN AQUARIA

For the distribution experiments (**I**), the light intensity was adjusted to above $0.2\ \mu mol\ m^{-2}\ s^{-1}$ for the illuminated part of the experimental unit and below $0.004\ \mu mol\ m^{-2}\ s^{-1}$ for the refuge part, based on the preference of *C. flavicans* for intensities below 5 lx (approximately $0.09\ \mu mol\ m^{-2}\ s^{-1}$) (Wagner-Döbler 1988). For the *Chaoborus* feeding experiments, the light intensities were adjusted to $0.04\ \mu mol\ m^{-2}\ s^{-1}$ (**III**).

For the fish feeding experiments, the light intensities were adjusted to $0.1\ \mu mol\ m^{-2}\ s^{-1}$ to mimic the twilight conditions known to be suitable for perch feeding under natural conditions (Pekcan-Hekim et al. 2005; Nurminen et al. 2007) (**II**). The light source in the aquaria was created by fluorescent lamps above the aquaria, and the light intensities were monitored with an LI-1400 datalogger equipped with an LI-192SA quantum sensor (LI-COR Biosciences, Lincoln, NE, USA) (**I-III**). Various turbidity levels (0, 30, and 60 nephelometric turbidity units (NTUs)) in the perch-feeding experiments were created, using kaolin clay (particle size < 5 μm) and measured with a YSI-6820 sonde equipped with a YSI-6136 turbidity sensor (YSI Inc., Yellow Springs, OH, USA) (**II**).

3.2.2   VISIBILITY CONDITIONS IN MESOCOSMS

The mesocosms were filled with filtered (50-μm mesh size net) water coming from the nearby humic Lake Majajärvi (**IV**). The water color in the ponds was 140 mg Pt L^{-1}. The LI-1400 datalogger and LI-192SA quantum sensor were used to determine the light conditions in the mesocosms during each sampling (**IV**).

Depending on the weather, the light intensity in the ponds 5 cm below the surface fluctuated between 100 and $600\ \mu mol\ m^{-2}\ s^{-1}$, the average value being

240 µmol m^{-2} s^{-1}. On the bottom, the average light intensity was 63 µmol m^{-2} s^{-1}. No differences between treatments were detected (analysis of variance for repeated measurements ANOVAR, p > 0.05); the average light extinction coefficient was 4.8 m^{-1} in the nonturbulent ponds and 4.9 m^{-1} in the turbulent ponds.

3.3 TURBULENCE CONDITIONS

Turbulence for the feeding experiments (**II-IV**) was generated with computer-controlled submersible pumps (Tunze Turbelle nanostream 6055; Tunze Aquarientechnik GmbH, Penzberg, Germany). A submersible pump is less likely to disturb the feeding of both fish and *Chaoborus* larvae than the oscillating grids that are more commonly used to create turbulence (Saiz et al. 1992; MacKenzie and Kiørboe 2000). Submersible pumps have been used in comparable studies (Clarke et al. 2005; Sluss et al. 2008; Lee et al. 2010). For the distribution experiments (**I**), both the submersible pump and an oscillating grid were used to create the turbulence.

Turbulence was measured with an acoustic Doppler velocimeter (ADV, 10-MHz ADVField; Sontek/YSI, San Diego, CA, USA). For each water flow a 25-Hz measurement for a period of 2 min was carried out in the middle of the water column at nine points around the aquaria (**I-III**) and the mesocosms (**IV**). From the data provided by the HorizonADV 1.20 (Sontek/YSI) the root-mean-square (*RMS*) velocities (cm s^{-1}), energy dissipation rates (ε, m^2 s^{-3}), and the Reynolds (*Re*) numbers were calculated (**I-IV**).

In all the laboratory experiments (**I-III**), the turbulence in addition to calm conditions was adjusted to cover a wide range of natural turbulence levels in lakes (Etemad-Shahidi and Imberger 2001; Saggio and Imberger 2001; G.-Tóth et al. 2011). The *RMS* velocities varied between 0.0 and 18.1 cm s^{-1} and the corresponding dissipation rates between 9.0×10^{-7} and 4.3×10^{-2} m^2 s^{-3} (**I-III**). For the mesocosm experiments, one intermediate turbulence level (*RMS* velocity of 1.4 cm s^{-1}, dissipation rate 5.6×10^{-6} m^2 s^{-3}) (**IV**) was selected in addition to calm conditions, based on the responses of *Chaoborus* and fish to turbulence in laboratory experiments (**I-III**). The background turbulent *RMS* velocity for the mesocosms with no added turbulence was 0.3 cm s^{-1} on average ($\pm$ 0.1 cm s^{-1}) with a corresponding dissipation rate of 4.6×10^{-8} m^2 s^{-3} (**IV**).

3.4 PREDATORS AND PREY

Chaoborus flavicans larvae were used in the experiments as invertebrate predators. Chaoborids are considered as some of the most abundant and important invertebrate predators in freshwater plankton communities (Riessen et al. 1984; Liljendahl-Nurminen et al. 2003). They are tactile ambush predators that use mechanoreceptors to detect prey-induced disturbances in the water (Horridge 1966; Riessen et al. 1984) and can coexist at high densities with fish if they can find refuge against fish predation (Liljendahl-Nurminen et al. 2003).

Fourth-instar *Chaoborus* larvae (body length of 10 ± 0.5 mm) used in the laboratory experiments were collected from Lake Hunttijärvi (60°45'N, 25°27'E),

southern Finland (**I**) and Lake Majajärvi (61°13'N, 25°12'E), southern Finland (**II**, **III**). Both lakes have abundant planktivorous fish stocks (e.g. perch and roach (Hagman et al. 2008; Estlander et al. 2009)). Third and fourth instars of *Chaoborus* larvae (collected from Lake Majajärvi) were used as invertebrate predators in the mesocosm study (initial density of 0.3 ind. L^{-1}) (**IV**).

In the *Chaoborus* feeding experiments (**III**), *Daphnia pulex* Leydig were used as prey. They were collected from a small pond situated in Helsinki, southern Finland (60°13'N, 16°00'E). Daphnids between 1.0 mm and 1.7 mm of total body length were selected to ensure that chaoborids could ingest them (Smyly 1980).

The fish for the experiments were caught by trap netting from lakes in the Evo district (61°13'N, 25°12'E) (**III**, **IV**). In laboratory experiments investigating fish feeding, planktivorous perch (total length 9.1 ± 1.7 cm) were used as predators (**II**). Perch (total length 8.0 ± 2.3 cm) and roach (total length 8.0 ± 2.1 cm) were used as vertebrate predators in the mesocosm experiments (three individuals of each species per pond with fish, resulting in a 34-kg ha^{-1} fish biomass) (**IV**). These two species were selected, due to their different foraging strategies. Perch are solely visually foraging predators (Sandström 1999), whereas cyprinids, such as roach, may benefit from filter feeding under low visibility conditions (Lammens et al. 1987) and are thus probably less sensitive to changes in visibility conditions. Both species are common in boreal dystrophic lakes (Rask et al. 1999).

A mix of the natural zooplankton community of Lake Majajärvi was collected and equal aliquots of zooplankton were added to each pond (**IV**). The zooplankton were allowed to acclimatize and develop for 7 days before the experiments were initiated.

3.5 SAMPLING AND ANALYSES

3.5.1 LABORATORY EXPERIMENTS

At the beginning of the experiments aimed to clarifying the effect of turbulence on *Chaoborus* distribution (**I**), 100 chaoborid ind. were added to the vertical cylinder or 200 chaoborid ind. were added to the aquarium and allowed to acclimatize for 30 min, after which turbulence was initiated. After 15 min, each experiment was terminated by dividing the experimental units into sections isolating the refuge areas from the remaining units. The chaoborids were collected from each section and counted. Three replicates of each turbulence treatment were run in a random sequence, the water in the experimental units was changed after each experiment, and each larva was used only once. For each treatment, three replicates were run in a random sequence.

For planktivorous perch feeding experiments (**II**), one fish was placed in the aquarium and left to acclimatize for 6 h to the turbulence and visibility conditions set in the trial. Each trial was initiated with the addition of prey, i.e. 200 *Chaoborus* larvae, and terminated after 30 min by removing the fish from the aquarium. After each trial, the perch were measured for length and weight and the number of larvae

consumed were counted in their stomachs. For each treatment, five replicates were run in a random sequence.

To determine the effect of turbulence on *C. flavicans* feeding (**III**), 10 larvae were placed in the aquaria and allowed to acclimatize for 5 min under adjusted turbulence conditions, after which *D. pulex* were added as prey. Prey densities of 3 and 10 ind. L^{-1} were tested for 30 and 120 min. Each experiment ended by capturing the larvae from the aquaria with a 50-µm net and preserving them in 4% formaldehyde. The crop contents of each larva were quantified (Swift and Fedorenko 1973). For each prey density and duration, five replicates were run in a random sequence.

3.5.2 MESOCOSM EXPERIMENTS

The experiments determining the effect of turbulence with different predation regimes on the zooplankton community (**IV**) were conducted as a 2×2×2 factorial design, with three replicates for each combination of turbulence and predators, leading to a total number of 24 ponds. The ponds were sampled at 4-d intervals for 6 weeks. Zooplankton samples were taken with a tube sampler (sample volume of 6 L per pond). The water was filtered through a 50-µm plankton net and the samples were preserved in 4% formaldehyde. The zooplankton samples were analyzed by inverted microscopy (Olympus CK40; 125x magnification; Olympus Corporation, Tokyo, Japan) and identified to species or genus level. The zooplankton biomasses were calculated from individual lengths, using length-weight regressions.

During each sampling, water temperature, dissolved oxygen (DO), and pH were determined from each pond (YSI 6600V2 sonde (YSI Inc.)). Total phosphorus (TP) and total nitrogen (TN) samples were taken with a tube sampler and analyzed, using the method of Koroleff (1979) with a Lachat autoanalyzer (QuickChem Series 8000; Lachat Instruments (Hach Company), Loveland, CO, USA). Chlorophyll *a* (Chl *a*) samples were taken, filtered through Whatman GF/C –filters, and analyzed spectrophotometrically (Shimadzu UV-260, UV-Visible Recording Spectrophotometer; Shimadzu Corporation, Tokyo, Japan) after extraction with ethanol (Finnish Standard Association 1993).

3.6 STATISTICAL ANALYSIS

To explore the effect of turbulence on the ability of *Chaoborus* larvae to exploit their refuges in the vertical and horizontal directions, linear and second-order polynomial regressions were fitted to the relationships between *RMS* velocity and the proportion of *Chaoborus* larvae in the refuge (**I**). The data were arcsine $\sqrt{x}$ -transformed to improve normality.

The effects of turbulence and turbidity on the proportion of *Chaborus* larvae consumed by perch were analyzed, using two-way analysis of variance (ANOVA) (**II**). Two-way ANOVA was also used for the percentage of *Chaoborus* larvae that consumed prey at each turbulence level and duration (arcsine $\sqrt{x}$ -transformed data) (**III**). Pairwise comparisons between turbulence levels were conducted with Tukey's

honestly significant difference (HSD) -tests (**III**). To distinguish the effect of turbulence on the postencounter processes of the predators, the proportion of prey items encountered that were eaten was estimated. A positive relationship between turbulence and feeding rate requires that the postencounter processes of predation (pursuit, attack, capture (Holling 1959)) are unaffected by turbulence (MacKenzie et al. 1994). The encounter rates predicted were determined according to Rothschild and Osborn (1988)

$$nc. \quad 2\frac{(u^2 \quad v^2 \quad 4w^2)}{(v^2 \quad w^2)^{1\,2}} \tag{1}$$

where N is the prey density per unit volume, R the reactive distance of the predator (perch 0.5, 1.0, and 3.0 cm (Richmond et al. 2004) (**II**); *Chaoborus* 0.5 cm (Pastorok 1980) (**III**)), u the swimming speed of the prey (*Chaoborus* 0.1 cm s^{-1} (Pastorok 1981) (**II**); *D. pulex* 0.25 cm s^{-1} (Pastorok 1980)(**III**)), v the swimming speed of the predator (perch 14.0 cm s^{-1} (**II**); *C. flavicans* 0.1 cm s^{-1} (**III**)), and w the *RMS* velocity (cm s^{-1}). The ratio of the number of prey items consumed to those encountered was calculated at each turbulence level for each turbidity level (**II**), and for both durations (**III**) that were tested and compared with calm conditions, i.e. zero turbulence at each treatment. Low ratios relative to calm conditions indicated a negative effect of turbulence on postencounter processes. The dependence of the ratio between consumed to encountered prey and turbulence was tested by either a linear (**II**) or nonlinear regression model (**II**, **III**).

The between-treatment differences in the initial zooplankton biomass in the mesocosms were studied by analyzing the results of the first sampling day with ANOVA (ln(x+1)-transformed data) (**IV**). The effects of the various treatments on the biomass and size class distribution of zooplankton and on the environmental variables were studied with ANOVAR, which accounts for the temporal autocorrelation between sequential samples. Pairwise comparisons between treatments were conducted with Bonferroni t-tests (**IV**).

Additionally, redundancy analysis (RDA; ter Braak and Looman 1994) was used to explore the biomasses of the various crustacean zooplankton taxa in mesocosms with regard to environmental data to detect the relative effects of different environmental factors in the response of zooplankton biomass (statistical software Canonical Community Ordination (CANOCO) 5 (ter Braak and Šmilauer 2002). A Monte Carlo permutation procedure (499 permutations) was used to assess the explanatory power of single variables. The environmental variables were log-transformed. Turbulence, fish, and *Chaoborus* were included as quantitative variables with values of 0 and 1. RDA allows partitioning of the influence of different environmental factors on the total variation (TV).

4   RESULTS

4.1 *CHAOBORUS* DISTRIBUTION ACROSS A TURBULENCE GRADIENT

The light environment affected the distribution of *C. flavicans* larvae (three-way ANOVA, $F_{18,53} = 56.87$, $p < 0.001$), such as when the experimental unit was illuminated the larvae tended to aggregate in the darkened section both in the vertical and horizontal directions. However, turbulence also affected the distribution of *Chaoborus* larvae in both directions (three-way ANOVA, $F_{18,53} = 7.58$, $p < 0.001$). The ability of *Chaoborus* larvae to use their vertical refuge decreased linearly with increasing turbulence (linear regression, $y = -0.0253x + 1.1726$, $R^2 = 0.42$, $F_{1,16} = 11.78$, $p = 0.0034$). Without turbulence, an average of 84% of the larvae were found in the refuge, while at the highest turbulence level (*RMS* velocity of 10.2 cm s^{-1}, dissipation rate 1.3×10^{-3} m^2 s^{-3}) an average of 61% occupied the refuge (Fig. 3a).

In the horizontal direction, the effect of turbulence on the distribution of larvae was even more pronounced. Without turbulence, on average of 86% of the larvae were found in the refuge, but the percentage decreased steeply with increasing turbulence. At *RMS* velocities of 5.4 cm s^{-1} and higher (corresponding to dissipation rates $\geq 10^{-5}$ m^2 s^{-3}), only 32–36% of the larvae were found in the refuge, suggesting that the larvae were randomly distributed around the aquarium (polynomial regression, $y = 0.0112x^2 - 0.1666x + 1.1346$, $R^2 = 0.849$, $F_{1,16} = 42.23$, $p < 0.001$) (Fig. 3a). The control treatments with uniform darkness revealed that the larvae were uniformly distributed around the experimental units, regardless of the turbulence level, resulting in a significant turbulence-light condition interaction (three-way ANOVA, $F_{18,53} = 4.29$, $p = 0.002$) (Fig. 3b).
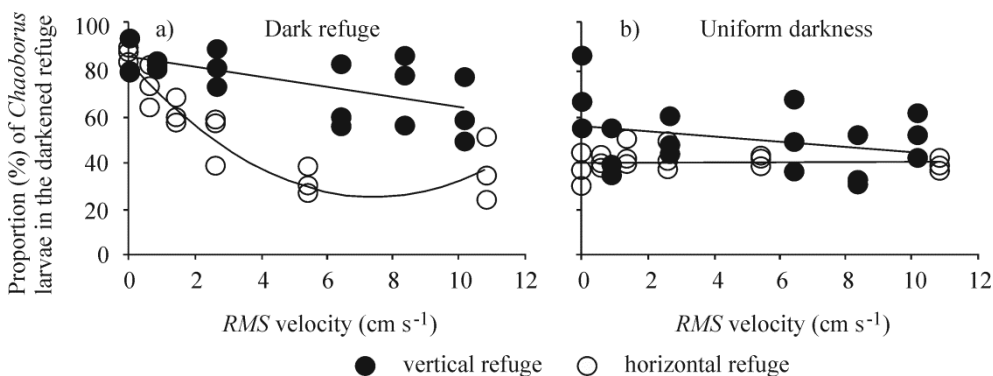

Fig. 3. Proportion of *Chaoborus* larvae in darkened vertical and horizontal refuges with respect to *RMS* velocity in a) light with a dark refuge and b) in uniform darkness (modified from **I**).

21

4.2 IMPACT OF TURBULENCE AND VISIBILITY CONDITIONS ON PLANKTIVOROUS FISH FEEDING

The aquarium experiments with different turbidity levels combined with a gradient of turbulence revealed that the proportion of *Chaoborus* larvae consumed by perch was significantly affected by *RMS* velocity (two-way ANOVA, $F_{4,60} = 2.675$, $p = 0.040$), turbidity (two-way ANOVA, $F_{2,60} = 10.622$, $p < 0.001$), and the interaction between *RMS* velocity and turbidity (two-way ANOVA, $F_{8,60} = 2.519$, $p = 0.020$).

In clear water the number of prey consumed was not affected by the *RMS* velocity (one-way ANOVA, $F_{4,20} = 0.29$, $p = 0.88$). However, with increasing turbulence the feeding efficiency of planktivorous perch was enhanced under low visibility conditions (Fig. 4).
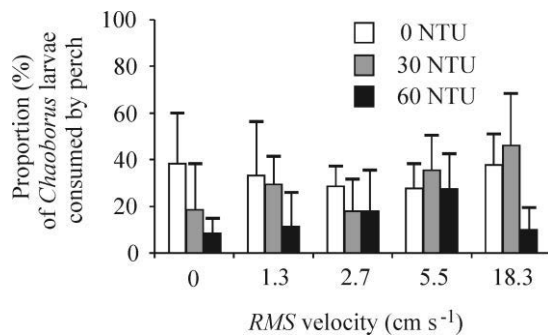

Fig. 4. Average proportion (+ standard deviation) of *Chaoborus* larvae consumed by perch under different turbulence (*RMS* velocity) and visibility (turbidity, NTU) conditions (modified from **II**).

The Rothschild and Osborn (1988) equation shows, that the encounter rate between predators and prey increases with increasing turbulence. The proportion of prey consumed to those encountered relative to calm conditions decreased significantly in clear water (linear regression: $y = -0.03x + 0.94$, $R^2 = 0.97$, $F_{1,3} = 110.954$, $p = 0.002$), whereas in 60 NTUs the proportion had a dome-shaped response to increasing turbulence (nonlinear regression (second-order polynomial): $y = -0.01x^2 + 0.21x + 0.95$, $R^2 = 0.99$, $F_{2,2} = 94.922$, $p = 0.010$) (Fig. 5). At an *RMS* velocity of 5.5 cm s^{-1}, the proportion of prey consumed to those encountered exceeded a 1.6-fold increase compared with calm conditions in 60 NTUs.

In 30 NTUs the lower turbulence levels seemed to increase the proportion of prey consumed to those encountered relative to calm conditions. However, no significant effect of turbulence could be observed (nonlinear regression (second-order polynomial): $y = -0.004x^2 + 0.05x + 1.08$, $R^2 = 0.72$, $F_{2,2} = 2.588$, $p = 0.279$) (Fig. 5).
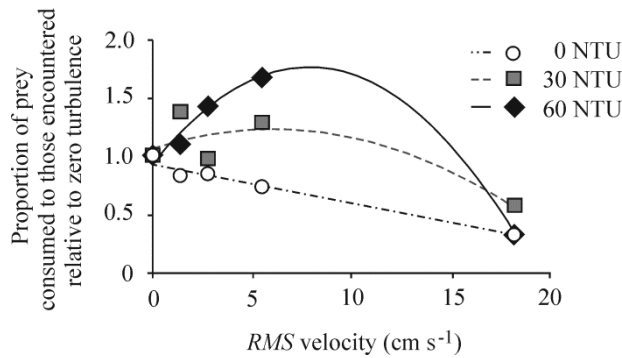
Fig. 1. Average proportion of *Chaoborus* larvae that perch consumed relative to those encountered (Rothschild and Osborn 1988) with respect to turbulence relative to calm conditions. Recalculated from **II**.

4.3 *CHAOBORUS* FEEDING UNDER TURBULENT CONDITIONS

The *Chaoborus* feeding was affected by turbulence (two-way ANOVA, $F_{5,110} = 5.707$, $p < 0.001$) and duration (two-way ANOVA, $F_{1,110} = 19.667$, $p < 0.001$). No interaction between turbulence and duration was observed (two-way ANOVA, $F_{5,110} = 0.206$, $p = 0.959$).

Under calm and intermediate turbulence conditions (*RMS* velocity 0–1.4 cm s^{-1}, dissipation rate $\leq 10^{-6}$ m^2 s^{-3}, respectively), the proportion of *Chaoborus* larvae feeding was 16–23% with a 30-min duration, and 33–39% with a 120-min duration. No increase in the feeding efficiency of *Chaoborus* larvae under intermediate turbulence levels compared with calm conditions was detected (Fig. 6). When the *RMS* velocity exceeded 3.1 cm s^{-1} (dissipation rate 10^{-5} m^2 s^{-3}), the feeding rate declined and differed from that at lower turbulence levels (Tukey's HSD, $p < 0.05$).
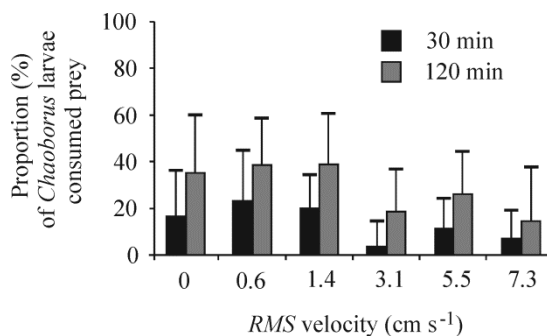

Fig. 6. Average proportion (+standard deviation) of *Chaoborus* larvae that consumed prey (*D. pulex*) across a turbulence gradient. Modified from **III**.

Larvae that had eaten consumed typically one and a maximum of two individuals of *D. pulex*. The conditional probability for a larva that consumed one prey item to consume another was 0.208. Turbulence did not affect the number of larvae consuming a second prey item (ANOVA, $F_{18,101} = 0.35$, $p = 0.883$).

23

The proportion of daphnids consumed to those encountered relative to calm conditions decreased exponentially with increasing turbulence both with the 30-min (logistic regression: $y = 0.62e^{-0.59x}$, $R^2 = 0.81$, $F_{1,4} = 17.486$, $p = 0.014$) and 120-min durations (logistic regression: $y = 0.63e^{-0.53x}$, $R^2 = 0.92$, $F_{1,4} = 46.651$, $p = 0.002$) (Fig. 7). The decrease in the proportion of prey consumed relative to zero turbulence was most prominent with *RMS* velocities exceeding 3.1 cm s^{-1}.
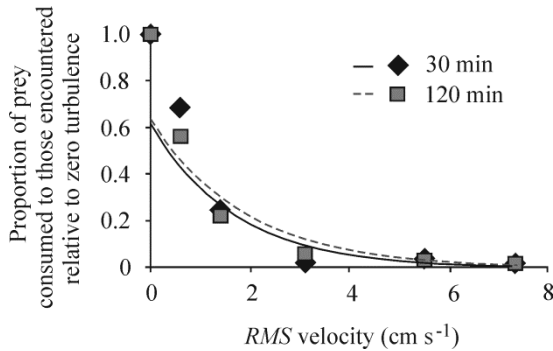

Fig. 7. Average proportion of *D. pulex* that *Chaoborus* larvae consumed to those encountered (Rothschild and Osborn 1988) with respect to turbulence relative to calm conditions. Recalculated from **III**.

4.4 INTERMEDIATE TURBULENCE COMBINED WITH HIGH WATER COLOR – EFFECTS OF VARIOUS PREDATORS ON ZOOPLANKTON

4.4.1 SPECIES COMPOSITION OF ZOOPLANKTON

During the study period the crustacean zooplankton in the mesocosms were dominated by cladocerans, *Bosmina* spp. Baird being the most abundant taxon (Fig. 8). In the analysis of the initial zooplankton biomass, there were no between-treatment differences in any of the taxa studied (one-way ANOVA, $p > 0.1$). Considering the whole study period, all analyzed taxa were affected by treatment (ANOVAR) ($F_{7,2080} = 14.949$, $p < 0.001$), sampling day ($F_{9,2080} = 23.346$, $p < 0.001$), as well as the treatment-day interaction ($F_{63,2080} = 1.335$, $p < 0.05$). Turbulence alone affected only on *Polyphemus pediculus* L., which also affected the total crustacean zooplankton biomass (Table 1).
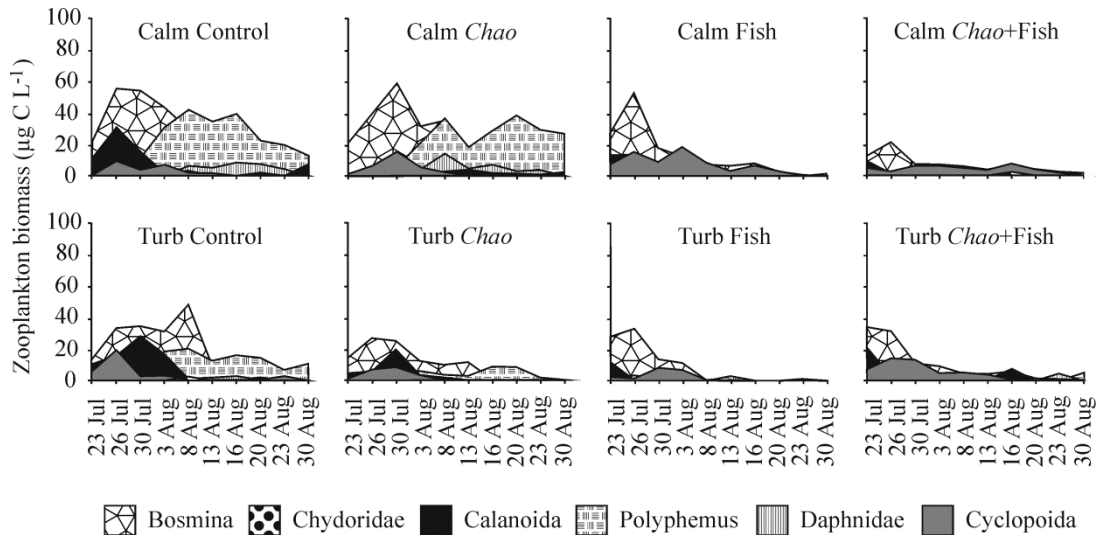
Fig. 8. Development of crustacean zooplankton biomass in the different treatments during the study period. Turbulence (Turb; dissipation rate 10^{-6} m^2 s^{-3}) was initiated after the sampling on July 23 and the predators were added after the sampling on July 26. Modified from **IV**.

Comparisons of different predation regimes in calm and turbulent treatments showed that with invertebrate predators, the effect of turbulence was strongest for cladocerans, whereas in a fish-dominated system the effect on cladocerans was weaker, but copepods were predominantly affected. All cladocerans, except chydorids, showed lower biomasses under turbulent than calm conditions when chaoborids were present (Fig. 8, Table 1). Copepods, on the other hand, were not affected by chaoborids. In the fish treatments, the biomass of bosminids and cyclopoids was lower under turbulent than under calm conditions (Fig. 8, Table 1). Cyclopoids were suppressed by fish predominantly under turbulent conditions; their biomass was reduced to 71% of that under predator-free conditions, whereas their biomass under calm conditions with fish increased steeply to 250% of that under predator-free conditions. No differences in zooplankton biomasses were detected between calm and turbulent conditions when both chaoborids and fish were included as predators.

Table 1. Pairwise between-treatment comparisons for differences in crustacean zooplankton biomass during the study period (**$p < 0.01$, *$p < 0.05$, - no significant difference). Modified from **IV**.

	Cladocera	Bosmina sp.	Polyphemus	Daphnidae	Chydoridae	Copepoda	Calanoida	Cyclopoida
Effects of turbulence alone								
Calm Control vs. Turb Control	**	-	**	-	-	-	-	-
Calm vs. turbulent water with different predators								
Calm *Chao* vs. Turb *Chao*	*	**	**	**	-	-	-	-
Calm Fish vs. Turb Fish	-	*	-	-	-	**	-	**
Calm *Chao*+Fish vs. Turb *Chao*+Fish	-	-	-	-	-	-	-	-

4.4.2 SIZE DISTRIBUTION OF ZOOPLANKTON

At the beginning of the experiment, the crustacean zooplankton in all the treatments were dominated by the small size classes 100–299 μm and 300–499 μm, which together formed > 70% of the total biomass of crustaceans (Fig. 9). Thereafter, in both control treatments and in calm treatments with chaoborids, the proportion of the small size classes decreased steeply, while the proportion of larger zooplankton increased (Fig. 9). In late August, the proportion of size classes 100–299 μm and 300–499 μm together was < 30% in all these three treatments. In the turbulent treatments with chaoborids, the reduction in small size classes was less clear, although towards the end of the study larger (> 500 μm) size classes tended to predominate. In both calm and turbulent treatments with fish, no seasonal trend in the size distribution of zooplankton was observed, but the proportions of the various size classes remained similar throughout the experiment. In both of these fish treatments, the proportion of size classes 100–299 μm and 300–499 μm together stayed above 60% throughout the experiment. In the calm and turbulent treatments including both chaoborids and fish, the proportions of the various size classes were similar to those of the fish treatments, without any trends during the experiment.

When the biomasses of the various size classes were compared between treatments, the only differences detected were between the calm and turbulent treatments with chaoborids in the proportion of size classes 500–699 μm and 700–999 μm (ANOVAR, Bonferroni t-tests, $p < 0.05$). Under calm conditions, differences were noted between chaoborids and fish as predators in the proportion of size class 700–999 μm. Under turbulent conditions, on the other hand, no significant differences between treatments were observed (ANOVAR, Bonferroni t-tests, $p > 0.05$).
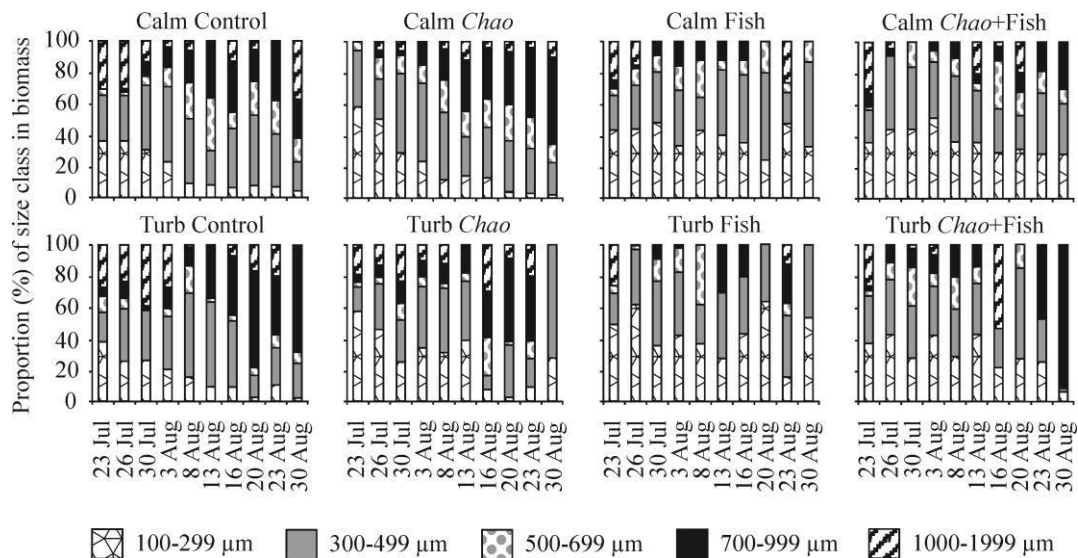

Fig. 9. Development of crustacean zooplankton biomass in the various treatments during the study period. Turbulence (Turb; dissipation rate 10^{-6} m^2 s^{-3}) was initiated after the sampling on July 23 and the predators (*Chao=Chaoborus*) were added after the sampling on July 26. Modified from **IV**.

4.4.3 EFFECT OF TURBULENCE AND VARIOUS PREDATORS ON ZOOPLANKTON BIOMASS WITH RESPECT TO OTHER ENVIRONMENTAL FACTORS

RDA revealed that the environmental variables measured explained 28% of the total biomass variation in the various zooplankton groups. Monte Carlo permutation tests of the RDA solution showed that all canonical axes were significant (T = 1.02, $F = 8.90$, $p = 0.002$). The first axis, where fish and *Chaoborus* together with their interactions with turbulence were associated, explained most of the TV (Fig. 10). Turbulence alone explained only 2.8% of the TV, whereas fish accounted for 11.9%. The biomass of the groups *Bosmina* spp., Daphnidae, *Polyphemus*, and Calanoida were negatively correlated with fish, whereas rotifers were positively correlated with fish. *Chaoborus* alone (0.3% of TV) did not correlate with the biomass of the various zooplankton groups, but the interaction of turbulence with chaoborids (1.8% TV) and turbulence with fish (3.8% TV) resulted in parallel effects. The interaction of chaoborids with fish explained 4.0% of the TV.

The environmental variables were associated with the second axis (Fig. 10). *Bosmina* spp., Calanoida, Cyclopoida, and Rotifera were positively correlated with temperature (6.0% TV) and pH (3.1% TV). Calanoids were negatively correlated with DO (1.5% TV).
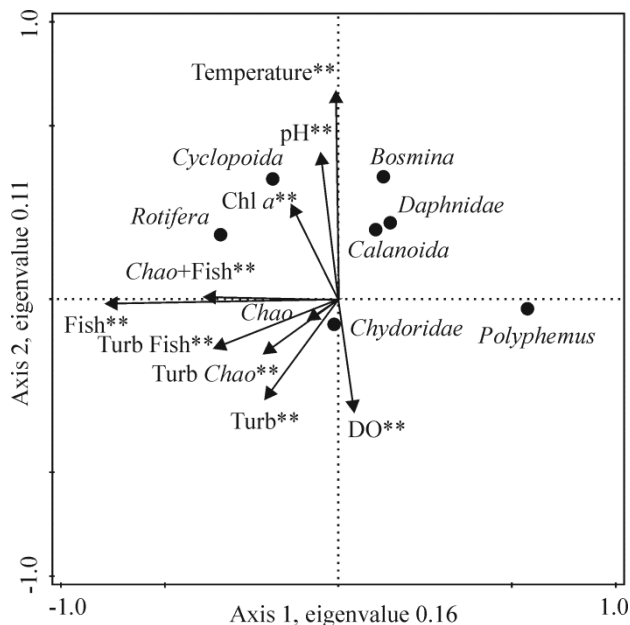

Fig. 10. Biplot of ordination model (RDA) results showing the relationships of the response variables (zooplankton biomass) to various environmental factors (Turb = turbulence; *Chao* = *Chaoborus*; DO = dissolved oxygen). Turbulence, fish, and *Chaoborus* were included as quantitative variables with values of 0 and 1. Asterisks indicate significant effects of the environmental factors (**$p < 0.01$).

For most of the study period, the water temperature fluctuated between 18 and 21°C, although in late July, the temperature temporarily reached 23 °C (Table 2). The water pH varied between 6.8 and 6.9. The concentration of DO varied between 8 and 9 mg L^{-1}. The between-treatment differences in temperature (ANOVAR,

$F_{21,50} = 1.362$, $p = 0.181$), pH (ANOVAR, $F_{20,45} = 0.414$, $p = 0.982$) and DO (ANOVAR, $F_{24,55} = 1.585$, $p = 0.08$) during the study period were insignificant. Thus, the positive correlation of the biomass of the various zooplankton taxa with these environmental parameters was associated with the seasonal succession of the zooplankton- rather than turbulence-mediated changes in these environmental parameters. Of the environmental variables, the Chl a concentration was positively correlated with fish; however, with the interaction of turbulence with fish the correlation was not observed. Among the treatments, however, no differences were observed in the Chl a concentration (ANOVAR, $F_{26,59} = 1.241$, $p = 0.244$), nor did turbulence alone affect the Chl a concentration in the mesocosms (ANOVAR, $F_{4,59} = 2.101$, $p = 0.097$)

Table 2. Average values (± standard deviation) of water temperature, dissolved oxygen (DO), pH, total phosphorus (TP), total nitrogen (TN), and chlorophyll a (Chl a) concentration in the various treatments (*Chao = Chaoborus*) during the study period under calm and turbulent (Turb) water.

Treatment	Temp (^{o}C)	DO (mg L^{-1})	pH	Chl a (µg L^{-1})
Calm Control	18.7±2.1	8.3±0.4	6.9±0.2	16.1±9.1
Calm *Chao*	18.7±2.1	8.3±0.5	6.9±0.2	14.9±8.0
Calm Fish	18.6±2.1	8.4±0.4	6.9±0.1	18.3±13.7
Calm *Chao*+Fish	18.5±2.0	8.3±0.5	6.9±0.1	18.5±11.4
Turb Control	18.8±2.1	8.7±0.3	6.9±0.1	13.3±6.4
Turb *Chao*	18.9±2.1	8.5±0.3	6.9±0.1	15.6±7.2
Turb Fish	18.7±2.1	8.6±0.3	6.8±0.1	17.0±7.9
Turb *Chao*+Fish	18.7±2.1	8.7±0.3	6.8±0.1	16.3±7.7

5 DISCUSSION

During recent decades, freshwater ecosystems in the Northern Hemisphere have experienced increased water brownification originating from the increased loads of DOC from the surrounding terrestrial environment (Hongve et al. 2004; Frey and Smith 2005). Additionally, erosion from the surrounding soils or resuspension of the sediment causes turbidity of the water, due to suspended inorganic particles, which is a prominent feature especially in shallow lakes (Evans 1994; Scheffer 1998; Horppila and Nurminen 2003; Lind 2003). Furthermore, visibility conditions in lakes have been predicted to decline, due to climate change-induced variations, e.g. in the vegetation of the surrounding catchment areas, precipitation, soil erosion, as well as turbulence-accelerated sediment resuspension (Horppila and Nurminen 2003; Hongve et al. 2004; Evans et al. 2005; Wrona et al. 2006; Granéli 2012). At the same time, climate models predict increasing wind and storm activities (Giorgi et al. 2004), resulting in increasing turbulent velocities in lakes. Additionally, predicted decrease in summertime cloudiness (Giorgi et al. 2004) may affect the turbulence conditions of lake ecosystems, due to intensifying nighttime convection. In small, sheltered lakes, e.g. those surrounded by forests, convection can be a larger mixed-layer turbulence source than wind shear (Nordbo et al. 2011; Read et al. 2012). Our results demonstrated that increasing turbulence together with varying visibility conditions can substantially affect the distribution and feeding of pelagic invertebrates, as well as the feeding efficiency of planktivorous fish.

5.1 *CHAOBORUS* DISTRIBUTION AND ITS IMPLICATIONS FOR FISH PREDATION

Our results demonstrated that turbulence affects *Chaoborus* distribution both in the vertical and horizontal directions. With increasing turbulence, a decreasing proportion of larvae were able to determine their position, because they were forced away from the darkened refuge.

Chaoborus larvae are relatively large and conspicuous, which makes them a favored prey item for planktivorous fish (Stenson 1980). In lakes with low visibility conditions, large hypolimnia often accompanied by anoxic conditions, provide refuges against fish predation (Liljendahl-Nurminen et al. 2003). The third and fourth instars of *C. flavicans* larvae are negatively phototactic and conduct vertical migrations, spending daytime in the darkness of the hypolimnion (Teraguchi and Northcote 1966; Parma 1971; Gliwicz et al. 2000). *Chaoborus* larvae tolerate low oxygen concentrations and can therefore inhabit the hypolimnia of stratified lakes during daytime and migrate to the epilimnion at night to forage on zooplankton (Luecke 1986; Voss and Mumm 1999; Liljendahl-Nurminen et al. 2003). The migrations of *Chaoborus* larvae are oriented mainly in the vertical direction (Teraguchi and Northcote 1966; Parma 1971; Gliwicz et al. 2000) and they are very efficient in regulating their vertical position. However, our results demonstrated that increasing turbulence influenced *Chaoborus* distribution in the vertical direction,

although rather high turbulent velocities were required to disturb a majority of the *Chaoborus* population (**I**). However, in investigating a clay-turbid lake, Malinen et al. (2001) discovered that wind-driven Langmuir circulations can force chaoborids from their hypolimnetic low-oxygen refuge to the epilimnion and estimated that one fifth of the *C. flavicans* population was forced upwards by these circulations (Fig.11a, b).
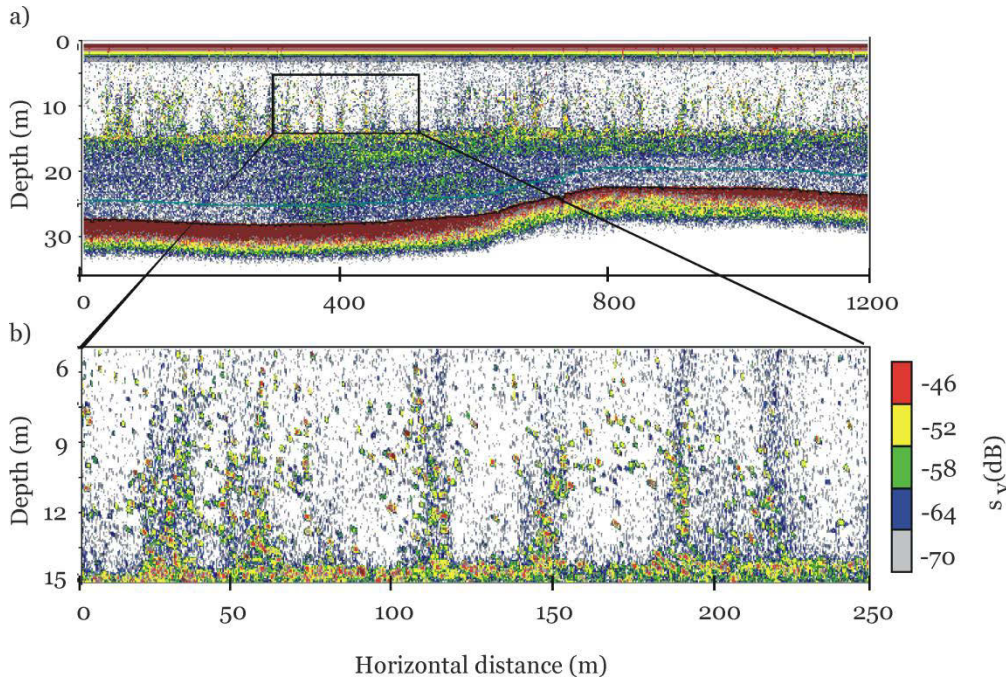

Fig. 11. Echograms from a study transect in clay-turbid Lake Hiidenvesi during a strong wind event (wind velocity 9 m s^{-1}). The colors represent different dB values of the volume backscattering strength (s$_v$), i.e. the echo integral of a small water volume. a) Echogram from the entire study transect, showing the highest density of *Chaoborus* larvae (yellow) in the metalimnion. The upwelling clouds of larvae can be clearly detected. b) A magnification showing smelts (separate large spots) concentrating in the upwelling clouds as well as at the edge of the *Chaoborus* population. Modified from Malinen et al. (2001).

Moreover, Malinen et al. (2001) discovered aggregation of European smelt (*Osmerus eperlanus* L.) in the low-oxygen concentrated metalimnion and also in the *Chaoborus* clouds forced to the epilimnion (Fig. 11b). The dissipation rate within the Langmuir circulations is at the level of 10^{-5} m^2 s^{-3} (Thorpe et al. 2003). Our experiments confirmed that at such turbulence levels, a proportion of *Chaoborus* larvae would be vertically displaced (**I**). At such levels, the feeding efficiency of planktivorous perch was also enhanced under low visibility conditions (**II**). The aggregation of smelts as observed in Malinen et al. (2001) strengthens our suggestion of the beneficial effect of high turbulence on the feeding efficiency of planktivorous fish under low visibility conditions. Given the combined responses of *Chaoborus* distribution and planktivorous perch feeding to turbulence, our results suggest that high turbulence can have two kinds of implications for planktivorous fish feeding. Firstly, turbulence may expose the prey in their vertical refuges and,

secondly, leave the larvae highly vulnerable to turbulence-induced horizontal dispersion, which decreases their ability to conduct antipredatory movements. The actual proportion of affected larvae is dependent on local factors, such as amplitude of the Langmuir cells and thermocline depth in relation to the location of chaoborid swarms (Ledbetter 1979). Langmuir circulation interacts with and often dominates other turbulent processes driving dispersion in the surface layer and engulfing stratified water in the mixed layer (Thorpe 2004). Our results support the theory that *Chaoborus* larvae are not able to escape from disturbing turbulence in all situations.

Chaoborids are also known to travel horizontally to avoid being captured by predators (O'Bryan and Forrester 1997). Our results demonstrated that increasing turbulence significantly affects the horizontal distribution of *C. flavicans* larvae (**I**). The ability of zooplankton to aggregate into prey patches to avoid predation and to conduct escape responses is dependent on their swimming strength with respect to local turbulence (Maar et al. 2003). Lee et al. (2010) also suggested that turbulence considerably affects the escape responses of invertebrate prey.

Although juvenile and adult fish are assumed to be unaffected by turbulence (Kiørboe and Saiz 1995, Eiane et al. 1997), our results showed that with increasing turbulence the consumption of *Chaoborus* larvae by planktivorous perch was enhanced under low visibility conditions (**II**). In clear water, no effect of turbulence on the feeding efficiency of perch was observed, which was attributed to the perch's short pursuit time and large reactive distance under sufficient visibility conditions (**II**). Given the responses of *Chaoborus* larvae to turbulent mixing (**I**), the enhanced feeding efficiency of perch under low visibility conditions was, however, not surprising and could be attributed to both increased encounter rates with chaoborids and to the diminished ability of *Chaoborus* to conduct predator escape responses. The threshold turbulence level (*RMS* velocity of 4.5 cm s^{-1}, corresponding to a dissipation rate of 10^{-5} m^2 s^{-3}) completely determining the horizontal distribution of *Chaoborus* larvae was similar to the level increasing perch feeding (**I**, **II**). The negative effect of turbulence on *Chaoborus* distribution intersects with the positive effect of turbulence on perch feeding under clay-turbid conditions (≥ 30 NTUs) when the *RMS* velocity exceeds 5 cm s^{-1} (approximate dissipation rate 10^{-5} m^2 s^{-3}), i.e. the probability of a prey individual to be consumed by perch becomes higher compared with the probability of a successful escape (Fig. 12).
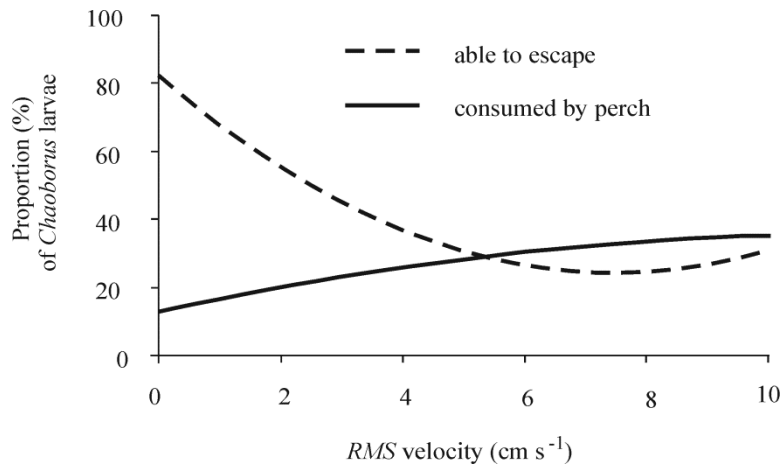
Fig. 12. Nonlinear regressions (second-order polynomial) fitted to the relationships between the *RMS* velocity and the proportion of *Chaoborus* larvae capable of determining their horizontal position (dashed line; $y = 1.0325x^2 - 15.43x + 82.144$) (data from **I**) and the proportion of available *Chaoborus* larvae consumed by planktivorous perch under clay-turbid conditions (black line; 30 and 60 NTUs combined; $y = -0.1704x^2 + 3.9349x + 13.049$)(data from **II**).

Such turbulence levels are commonly found in lake ecosystems (Etemad-Shahidi and Imberger, 2001; Saggio and Imberger 2001; G.-Tóth et al. 2011). Horppila et al. (2004) showed that turbidity exceeding 30 NTUs together with low light levels provides an efficient daytime refuge for *Chaoborus* larvae against fish predation. Our present results, however, suggest that turbulence can counteract the refuge effect of low visibility conditions; the feeding efficiency of planktivorous fish is enhanced as encounters with prey increase, whereas the ability of prey to escape predators weakens simultaneously with dissipation rates approaching 10^{-5} m^2 s^{-3}. This is especially likely in the mixed surface-water layer where turbulence is usually considerably stronger than in the deep-water layers (e.g. Imboden and Wüest 1995; Maar et al. 2003; Bouffard et al. 2012), easily exposing chaoborids to turbulence levels exceeding their capability for resisting water movements.

Strong stratification in lakes acts to damp out or inhibit turbulence (Denman and Gargett 1983). Although surface-layer turbulence is usually considerably stronger than turbulence in the meta- and hypolimnion (Imboden and Wüest 1995; Bouffard et al. 2012), elevated dissipation rates within the metalimnion, in addition to Langmuir circulation, result from Kelvin and Poincaré waves, as well as severe wind forcing (Saggio and Imberger 2001; Preusse et al. 2010; Bouffard et al. 2012). The dissipation rates measured within the metalimnion are in the range of 10^{-5} to 10^{-9} m^2 s^{-3} (MacIntyre 1993; Etemad-Shahidi and Imberger 2001; Saggio and Imberger 2001). *Chaoborus* larvae use the meta- and hypolimnion during the day to protect themselves from fish predation. High turbidity combined with low oxygen concentrations in metalimnion provide the most efficient protection against fish predation (Horppila et al. 2004, Liljendahl-Nurminen et al. 2008). Many fish species are intolerant to low oxygen concentrations, and hypoxic water layers thus provide a physiological refuge for prey from fish that avoid low oxygen concentrations (Liljendahl-Nurminen et al. 2008). Yet, there are examples in the environment in

which fish conduct short visits to hypoxic water layers to search for prey (Rahel and Nutzman 1994; Malinen et al. 2005). In such habitats, the time a predator spends foraging is limited, and therefore factors affecting the detection of prey and the probability of encounter become more important (Liljendahl-Nurminen et al. 2008). The situation is illustrated in Figure 13: the time (E) fish can be exposed to such conditions decreases with decreasing oxygen concentration. The time needed for searching for prey in calm water (S×C) increases with decreasing water clarity. Capturing prey is possible when $E \geq S \times C$, whereas all circumstances left of the intersection point ($E < S \times C$) are unsuitable for successful feeding in the metalimnion since fish have to escape the low-oxygen levels before any prey have been captured (Liljendahl-Nurminen et al. 2008). In introducing turbulence to the model of Liljendahl-Nurminen et al. (2008), the intersection point is relocated, consequently reducing unsuitable circumstances for fish feeding as the time needed for searching for prey (S×T) decreases, due to turbulence (Fig. 13).
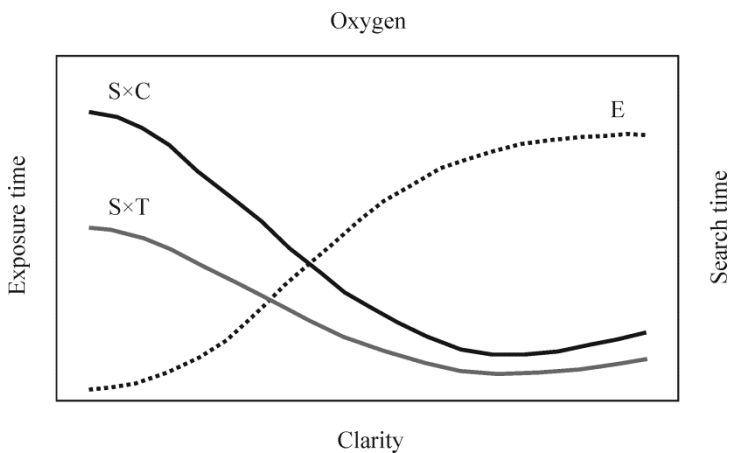

Fig. 13. A schematic presentation of the effects of a low-oxygen, and visually poor, refuge on the foraging of fish. The oxygen concentration limits the exposure time (E; dotted line), whereas water clarity affects the time required for searching for the prey (S×C; black line). The E curve is drawn according to the dependence of fish blood-oxygen saturation on the water oxygen level (Cameron 1971), which is indicative of limiting oxygen conditions for fish (Davis 1975). The S×C curve is drawn according to the model describing the effect of turbidity on the prey capture rate of fish feeding on *Chaoborus* larvae (Horppila et al. 2004). With increasing turbulence, the time needed searching for prey shortens (S×T, grey line), due to increasing encounter rates and weakening escape responses of prey items (**I**). Modified from Liljendahl-Nurminen et al. (2008).

The present results suggest that turbulence can interfere with the relationship between exposure time and search time by shortening the time needed to search for prey (**I**, **II**). Foraging of fish can be diminished through decreased encounter rates (Gerritsen and Strickler 1977; Utne-Palm 2002). Under low visibility conditions, increased searching activity was detected for certain fish species (Meager et al. 2005), suggesting that increased activity may counteract the reduced reaction distances. Our results suggested that turbulence can benefit fish feeding in degraded visibility and probably compensate for the time lost searching for the prey (**II**). Both horizontal distribution of *Chaoborus* larvae and the feeding efficiency of planktivorous perch were affected by a dissipation rate exceeding 10^{-5} m^2 s^{-3}, a level

that can be detected within the metalimnion (MacIntyre 1993; Etemad-Shahidi and Imberger 2001; Saggio and Imberger 2001). Consequently, the exposure time of planktivorous fish to hypoxic conditions may shorten, and the vulnerability of *Chaoborus* larvae to fish predation can increase indirectly due to turbulence, even if they are able to exploit the vertical refuge. Such a phenomenon was also possibly detected in Malinen et al. (2001), since during a turbulent event smelts aggregated not only in the *Chaoborus* clouds, but also in the low-oxygen metalimnion (Fig. 11a, b).

5.2 *CHAOBORUS* FEEDING UNDER TURBULENCE

With respect to feeding success, it has long been considered that increasing turbulence has a dome-shaped effect on planktonic organisms (Saiz et al. 1992; Kiørboe and Saiz 1995; Saiz and Kiørboe 1995; Irigoien et al. 2000). Under low and intermediate turbulence levels, turbulence enhances contact rates (Rothschild and Osborn 1988) and should consequently increase ingestion rates, while at high levels turbulence impairs the ability of organisms to detect and capture prey (MacKenzie et al. 1994; Kiørboe and Saiz 1995; Saiz and Kiørboe 1995). With a single species experiment using *D. pulex* as prey, our results demonstrated a controversial effect of turbulence on feeding of fourth-instar *Chaoborus* larvae (**III**). The expected increase in the feeding efficiency of *Chaoborus* larvae was not detected under intermediate-turbulence conditions, whereas high turbulence (*RMS* velocity exceeding 3.1 cm s^{-1}, dissipation rate 10^{-5} m^2 s^{-3}) decreased the proportion of larvae consuming prey. With wind speeds approaching 10 m s^{-1}, such high turbulence levels occur in shallow lakes (Baranyai et al. 2011; G.-Tóth et al. 2011) and probably also in the surface mixed layers of stratified lakes.

A positive relationship between turbulence and feeding rate requires the assumption that the postencounter processes of predation are unaffected by turbulence (MacKenzie et al. 1994). High turbulence can interfere with the feeding current of a predator, or move the prey out of the encounter distance before the predator has time to initiate an attack (Sundby and Fossum 1990; Kiørboe and Saiz 1995). The sensitivity of planktonic organisms' feeding rates to turbulence can be very dependent on the feeding behavior of the predator (Kiørboe and Saiz 1995; Saiz and Kiørboe 1995). An ambush sit-and-wait predator like *Chaoborus* is almost stationary and exhibits no apparent orientation behavior before an attack (Pastorok 1981). The pursuit time for *Chaoborus* is assumed to be negligible (Pastorok 1980; Pastorok 1981). Consequently, it is unlikely that the decline in their feeding efficiency observed in our study (**III**) at high turbulence levels occurred because of the advection of prey out of the reactive zone. Instead, the position of the predator may be important for successful ingestion. The turbulence level causing horizontal displacement of *Chaoborus* larvae (**I**) was close to the level reducing their feeding efficiency (**III**), since the food intake could have been interrupted as the predators began whirling in the water.

Although the laboratory experiments did not indicate the expected positive effect of low and intermediate turbulence levels on *Chaoborus* feeding (**III**), the mesocosm

experiments (**IV**) with a versatile zooplankton prey community, on the other hand, showed that under intermediate turbulence, the third and fourth instars of *Chaborus* larvae significantly affected the zooplankton community structure. The difference between the diverse results of intermediate turbulence for *Chaborus* feeding can probably be attributed to both prey size and prey swimming ability. Although the daphnids used in the feeding experiments in aquaria (**III**) were in the size range that chaoborids can ingest (Smyly 1980), they were remarkably larger and closer to *Chaborus'* ingestion limit (Smyly 1980) than individuals (e.g. *Bosmina* spp.) comprising the mesocosm zooplankton community (**IV**). The mesocosm experiments showed that *Chaborus* larvae affected the zooplankton community structure, and their selective feeding towards cladocerans increased under intermediate turbulence. Their size selectivity, on the other hand, was not different from that under calm conditions, and they rather preferred the small-sized cladocerans (< 500 μm body length) (**IV**). In laboratory experiments, the conditional probability for *Chaborus* ingesting more than one large *Daphnia* revealed that if a *Chaborus* consumed a single one prey item, it probably became satiated and did not consume a second one (**III**). With a prey population of varying size distribution, *Chaborus* larvae can have a more pronounced effect, since they can ingest more prey items before satiation. The results of the mesocosm experiments (**IV**) were in concordance with the assumption that intermediate turbulence may enhance the feeding rate of planktonic organisms, due to increased encounter rates (Rothschild and Osborn 1988; Saiz et al. 1992; Kiørboe and Saiz 1995; Saiz and Kiørboe 1995; Irigoien et al. 2000).

The ability of zooplankton to aggregate into prey patches to avoid predation and to make antipredatory movements is dependent on their swimming strength with respect to local turbulence (Maar et al. 2003). Turbulence affects especially the distribution of small organisms and weak swimmers, such as ciliates and nauplii (Maar et al. 2003). The swimming behavior of zooplankton, both in speed and path geometry, varies with different levels of turbulence (Saiz and Alcaraz 1992; Seuront et al. 2004). In the mesocosm experiments (**V**), bosminids especially were depressed by chaoborids, which was in accordance with the feeding habits of *C. flavicans* larvae: the third and fourth instars of *C. flavicans* larvae usually show a strong positive selection for bosminids (Elser et al., 1987; Stenson 1990; Liljendahl-Nurminen et al., 2003). The positive selection for bosminids was even more pronounced under intermediate turbulence combined with calm conditions, suggesting that the escape behavior of *Bosmina* spp. may have been affected by turbulence. The escape response of *Bosmina* from predators is to sink passively (Kerfoot 1975), whereas daphnids and copepods have both efficient and rapid escape responses by actively changing direction, hopping, and swimming (Saiz and Alcaraz 1992; Browman et al. 1989; Brewer et al. 1999). The passive behavior of zooplankton under turbulent conditions may result in advective transportation along the turbulent water motion rather than passive sinking (Saiz and Alcaraz 1992). Additionally, the handling time and strike efficiency of *Chaborus* larvae decrease with increasing prey size (Swift and Fedorenko 1975; Pastorok 1981). Consequently the chances for bosminids of being captured by chaoborids were assumed to be high as a result of their small size and passive escape responses. In the mesocosm

experiments, chaoborids indeed chose bosminids over more strongly swimming daphnids (**IV**). Consequently, the higher capability of daphnids for conducting predator escape responses under turbulence probably explains the lack of increase in the feeding efficiency of chaoborids under the intermediate turbulence observed in the aquarium experiments (**III**).

5.3 IMPACT OF VARIOUS PREDATION REGIMES ON ZOOPLANKTON UNDER TURBULENT CONDITIONS

It is generally believed that invertebrate predators can only play a significant role in regulating the zooplankton communities if the density of planktivorous fish is very low (Scheffer 1998). In lakes inhabited by invertebrate predators and fish, the effect of each is reduced due to intraguild predation. However, under low visibility conditions the importance of the pelagic invertebrate *Chaoborus* can be substantial, despite abundant planktivorous fish stocks, due to the shelter provided by obscurity and low-oxygen water layers (Liljendahl-Nurminen et al. 2003; Wissel et al. 2003). In such lakes, increasing turbulence may strongly affect the top-down control of zooplankton via enhancement of invertebrate predation and may possibly even turn the dominance from fish to invertebrates.

The zooplankton community in the mesocosms was dominated by cladocerans, with the seasonal succession of both cladocerans and copepods following the typical succession in Lake Majajärvi during late July and August (Estlander et al. 2009). No differences between treatments were found for the environmental parameters correlating with the zooplankton biomass (temperature, DO, pH, and Chl *a*), indicating that the between-treatment differences in zooplankton biomass were caused by different predator treatments combined with turbulent conditions, instead of these other environmental parameters. Intermediate turbulence alone negatively affected the biomass of *P. pediculus* (**IV**), a cladoceran species known as an invertebrate predator (Packard 2001). The decrease in *P. pediculus* under turbulent conditions was expected, because it is a species inhabiting sheltered stagnant habitats and is very vulnerable to environmental stress (Butorina 1986; Packard 2001).

At the same time, comparisons of fixed predation regimes in the calm and turbulent mesocosm treatments showed that with invertebrate predators, the effect of turbulence was strongest for cladocerans, whereas in a fish-dominated system the effect on cladocerans was weaker, but copepods were especially affected (**IV**). The *Chaoborus* density used in the mesocosms was moderate (119 ind. m^{-2}) (**IV**), whereas in some lakes the densities can be extensively higher, easily exceeding 10,000 ind. m^{-2} (Liljendahl-Nurminen et al. 2003; Horppila and Liljendahl-Nurminen 2005). In such lakes the combined effect of turbulence and chaoborus predation may result in substantial consequences at lower trophic levels.

Planktivorous fish prefer cladocerans over copepods (Drenner et al. 1978; Tolonen et al. 2000), which has been attributed to differential capture probabilities (Drenner et al. 1978). In the presence of fish, the decrease in herbivorous cladocerans results in increasing Chl *a* concentration (Carpenter et al. 1985; Šorf et al. 2014). In accordance, cladocerans under calm conditions were substantially

reduced by fish, whereas the copepod biomass together with Chl *a* concentration was positively correlated with the presence of fish (**IV**). However, under turbulent conditions the correlation disappeared and the copepod biomass was substantially supressed by fish, whereas cladocerans in addition to Chl *a* concentration were less affected. Cladocerans can substantially affect phytoplankton communities (e.g. Lampert et al. 1986), and changes in selective feeding of fish, due to turbulence, may considerably affect the phytoplankton populations. Comparable results for food selection of planktivorous fish were obtained in another experiment focusing on the effect of water quality and turbulence; in highly colored water planktivorous perch prefer copepods over cladocerans in the presence of turbulence (Z. Pekcan-Hekim unpubl.). At the same time, the size-selective feeding of fish on zooplankton was affected by turbulence, since cyclopoid copepods were nearly twice the size of bosminids (preferred by fish in addition to *P. polyphemus* under calm conditions) (**IV**). In concordance, Dower et al. (1998) found that larval fish selected on average larger zooplankton under turbulent instead of calm conditions.

The dissipation rate of turbulent kinetic energy applied in the mesocosm experiments was of the order $10^{-6}\,m^2\,s^{-3}$ (**IV**). Saiz and Alcaraz (1992) showed that such turbulence levels may affect the swimming habits of copepods, which may increase their activity and escape responses under turbulent conditions. Under low visibility conditions, increased activity of zooplankton prey enhances the chances of predators to detect them (von Ende and Dempsey 1981). On the other hand, copepods use their mechanosensors to detect the approaching predators. Hydrodynamic motion caused by turbulence may interfere with the sensitivity of copepods in detecting hydrodynamic disturbances in water (Yen and Strickler 1996) caused by the predators. A combination of increased activity and decreased sensitivity to predator-induced disturbances in the water may have caused the higher vulnerability of copepods to fish predation under turbulent conditions than under calm conditions (**IV**). Nevertheless, although the selective feeding of planktivorous fish appeared to be affected by the combined effect of turbulence and low visibility (**IV**; Z. Pekcan-Hekim unpubl.), the overall effect of fish on zooplankton biomass was not affected by intermediate turbulence (**IV**).

In systems inhabited by both invertebrates and fish as predators, the co-occurrence often leads to intraguild predation in which the intraguild prey is preyed upon by fish (Holt and Polis 1997). Perch and roach feed extensively on *C. flavicans* larvae when they are available (Eie and Borgstrøm 1981; Haertel and Eckmann 2002). The mesocosm experiments with a modest *Chaoborus* density showed that no differences between fish treatments and treatments including both chaoborids and fish as predators were detected (**IV**). Thus, the *Chaoborus* predation was probably limited by intraguild predation (**IV**). In numerous lakes, however, due to the refuges provided by low-oxygen layers, the *Chaoborus* densities can be considerably higher, due to which invertebrates can be the main predators of zooplankton despite the presence of fish (Liljendahl-Nurminen et al. 2003). In such lakes, intermediate turbulence may strongly affect the top-down control of zooplankton via enhancement of invertebrate predation and may possibly even turn the dominance from fish to invertebrates with possible consequences for lower trophic levels.

In many aquatic ecosystems, zooplankton are important secondary producers, since they provide a crucial link in energy transfer between primary producers and planktivorous predators (Chassot et al. 2010). Zooplankton populations are affected both by predation and resource availability (Nicolle et al. 2011) and the quality of food can substantially affect the grazing zooplankton. In marine environments, the Chl *a* concentration respond positively to turbulence (Iversen et al. 2010). Our results did not indicate an increase in the Chl *a* concentration in humic water due to turbulence, suggesting that the amount of food (resources) available for zooplankton was similar in all treatments, whereas the predators had a much more pronounced effect on zooplankton biomass (**IV**). However, the phytoplankton species composition in the mesocosms was not studied (**IV**). Theory and field experiments indicate that changes in turbulent mixing may shift competition for light and nutrient uptake rate between phytoplankton species and influence species composition (Thomas and Gibson 1990; Huisman et al. 2004; Metcalfe et al. 2004). Changes in phytoplankton community composition can directly affect the food quality of herbivorous zooplankton (Suikkanen et al. 2013), since the various phytoplankton groups are exploited differently as food sources for zooplankton taxa (e.g. Lehman and Sandgren 1985; Ahlgren et al. 1990; Sommer et al. 2001). Additionally, bacterioplankton play an important role in energy transfer from allochthonous humic matter to higher trophic levels, especially in dystrophic lakes (Jones 1992; Sarvala et al. 1999 with references). Variations in turbulence can also modify the bacterioplankton community structure in aquatic ecosystems (Moeseneder and Herndl 1995; Metcalfe et al. 2004). If turbulence affected the community structure and species composition of lower trophic levels, it could lead to considerable changes in the zooplankton populations, due to differential preferences for variable resources (Lehman and Sandgren 1985; de Bernardi and Giussani 1990). Changes in the bacterio- and phytoplankton community structure, due to turbulence, may severely impact the higher trophic levels through associations with the herbivorous zooplankton community and its efficacy in energy transfer. Hence, further research on the effect of turbulence on the lower trophic levels and its implications for the selective feeding of zooplankton are needed.

6 CONCLUSIONS

Increasing turbulence disturbed both the vertical refuge use and the ability of pelagic invertebrates (*C. flavicans*) to conduct horizontal movements (**I**), consequently leaving them highly vulnerable to predation, especially in surface-water layers where turbulence is usually considerably higher than in deeper water layers. Although turbulence is usually lower in the meta- and hypolimnion, turbulence levels exceeding that at which *Chaoborus'* ability to escape from predators is weakened have been observed within the stratified water layer (dissipation rate $\geq 10^{-5}\,\mathrm{m^2\,s^{-3}}$ (**I**, **II**)). As a consequence of *Chaoborus'* lessened ability to escape predators, the unexpected phenomenon in the studies was the significant, positive interaction of turbulence and visibility conditions on planktivorous fish feeding (**II**, **IV**). The proportion of chaoborids consumed under turbid and turbulent conditions showed a dome-shaped response, being highest with the dissipation rate of turbulent energy exceeding $10^{-5}\,\mathrm{m^2\,s^{-3}}$ (**II**). This was attributed to increased encounter rates between predators and prey, as well as difficulties of chaoborids in escaping predators under high turbulence (**I**). In clear water, increases in encounter rates or difficulties in prey escape responses did not benefit the feeding of fishes, due to their long reaction distance and short pursuit time (**II**). Our novel findings challenged the previous assumption that fish larger than a few centimeters in body length are unaffected by turbulence. Our results suggested that turbulence may compensate for the time a fish loses in searching for prey under low visibility conditions (**II**). Turbulence also affected the selective feeding of planktivorous fish; intermediate turbulence (dissipation rate $10^{-6}\,\mathrm{m^2\,s^{-3}}$) increased predation on copepods while predation on herbivorous cladocerans was smoothened (**IV**). Turbulence under low visibility conditions not only benefits planktivorous fish feeding, but may also change the dominance of the various zooplankton taxa via selective predation, with possible consequences for the lower trophic levels.

In concordance with this theory and previous studies, intermediate turbulence (dissipation rate $10^{-6}\,\mathrm{m^2\,s^{-3}}$) benefited invertebrate predators, such as *Chaoborus flavicans* feeding, but only when introduced to a naturally versatile zooplankton community (**III**, **IV**). The combined effect of turbulence and *Chaoborus* was strongest for cladocerans, which is notable, because in lakes they are able to significantly affect phytoplankton communities. Thus, in circumstances dominated by *Chaoborus* larvae as invertebrate predators, a modest increase in turbulence can substantially influence herbivorous zooplankton (**IV**). High turbulence (dissipation rate exceeding $10^{-5}\,\mathrm{m^2\,s^{-3}}$), on the other hand, degraded *Chaoborus* feeding (**III**), a phenomenon also observed in copepods as well as ichthyoplankton. At such turbulence levels the ability of *Chaoborus* larvae to determine their position was also weakened (**I**).

Decreasing visibility conditions and, on the other hand, increasing turbulence conditions are both predictable changes in the abiotic environment of lakes (Pryor et al. 2005; Samuelsson 2010). This thesis points out that turbulence together with varying visibility conditions can have variable implications for planktivorous

predation and should thus be treated as a significant factor in food web studies. Furthermore, intermediate turbulence together with contemporaneous increases in water color may possibly cascade to primary producers via effects on predation. Depending both on the dominant planktivores present and the magnitude of these changes in abiotic factors, significant consequences may occur in the lower trophic levels with possible implications even for cascading trophic interactions.

ACKNOWLEDGEMENTS

I also wish to acknowledge all my friends outside the department, especially the three dearest ones: Kati, Laura, and Salla that I've had the pleasure of having in my life ever since elementary school; thank you for always being there and bringing so much joy in my life.

This thesis is dedicated to my parents, who always pushed me towards the academic career. I want to thank my whole beloved family (Merja, Samuli, Marianna and Arttu) for all the help and support they provided, and for successfully showing keen interest in my work. Special thanks go to my sister Marianna, who assisted with some sampling and with her incredible luck also managed to fish our drowned sampling gear back. I also want to thank my dad Samuli for his never-ending interest and desire to speak science.

My greatest gratitude belongs to my husband Masa, the love of my life. Thank you for all your humor, support, foolery, patience, love, and understanding during this process. Thank you for keeping me going and making my life so much more than just studying worms. I wish you a happy wedding anniversary. In the following years, I promise we'll do something apart from my work to celebrate. Thank you for being. You are my everything ♥

REFERENCES

Ahlgren, G., L. Lundstedt, M. Brett, and C. Forsberg. 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. J. Plankton Res. 12: 809-818.

Aksnes, D.L. and J. Giske. 1993. A theoretical model of aquatic visual feeding. Ecol. Model. 67: 233-250.

Allan, J.D. 1973. Competition and the relative abundances of two cladocerans. Ecology 54: 484-498.

Andersen, V., A. Gubanova, P. Nival, and T. Ruellet. 2001. Zooplankton community during the transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of wind events. 2. vertical distributions and migrations. J. Plankton Res. 23: 243-261.

Anderson, D.M., P.M. Glibert, and J.M. Burkholder. 2002. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. Estuaries 25: 704-726.

Baranyai, E., L. G.-Tóth, A. Vári, and Z.G. Homonnay. 2011. The effect of variable turbulent intensities on the distribution of zooplankton in the shallow, large Lake Balaton (Hungary). Knowl. Manag. Aquat. Ec. 400: 1-13.

Bouffard, D., L. Boegman, and Y.R. Rao. 2012 Poincaré wave-induced mixing in a large lake. Limnol. Oceanogr. 57: 1201-1216.

Brett, M.T., and C.R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. Science (Washington DC) 275: 384-386

Brewer, M.C., P. Dawidowicz, and S.I. Dodson. 1999. Interactive effects of fish kairomone and light on *Daphnia* escape behavior. J. Plankton Res. 21: 1317-1335.

Brooks, J.L., and S.I. Dodson. 1965. Predation, body size and composition of the plankton. Science 150: 28-35.

Browman, H.I., S. Kruse, and W.J. O'Brien. 1989. Foraging behavior of the predaceous cladoceran, Leptodora kindti, and escape responses of their prey. J. Plankton Res. 11: 1075-1088.

Burks, R.L., D.M. Lodge, E. Jeppesen, and L. Lauridsen. 2002. Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. Freshw. Biol. 47: 343-365.

Butorina, L.G. 1986. On the problem of aggregations of planktonic crustaceans (*Polyphemus pediculus* (L.), Cladocera). Arch. Hydrobiol. 105: 355-386.

Cameron, J.N. 1971. Oxygen dissociation characteristics of the bood of rainbow trout, *Salmo gairdneri*. Comp. Biochem. Physiol. 38: 699–704.

Carpenter, S.R., J.F. Kitchell, and J.R. Hodgson. 1985. Cascading Trophic Interactions and Lake Productivity. BioScience 35: 634-639.

Carpenter, S.R., and J.F. Kitchell. 1988. Consumer control of lake productivity: large-scale experimental manipulations reveal complex interactions among lake organisms. BioScience 38: 764-769.

Chassot, E., S. Bonhommeau, N.K. Dulvy, F. Mélin, R. Watson, D. Gascuel, and O. Le Pape. 2010. Global Marine primary production constrains fisheries catches. Ecol. Lett. 13: 495-505.

Clarke, R.D., E.J. Buskey, and K.C. Marsden. 2005. Effects of water motion and prey behavior on zooplankton capture by two coral reef fishes. Mar. Biol. 146: 1145-1155.

Confer, J.L., G.L. Howick, M.H. Corzette, S.L. Kramer, S. Fitzgibbon, and R. Landesberg. 1978. Visual predation by planktivores. Oikos 31: 27-37.

Cuker, B.E. 1993. Suspended clays alter trophic interactions in the plankton. Ecology 74: 944-953.

Davis, J.C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. J. Fish. Res. Board. Can. 32: 2295–2331.

Davis, C.S., G.R. Flierl, P.H. Wiebe, and P.J.S. Franks. 1991. Micropatchiness, turbulence and recruitment in plankton. J. Mar. Res. 49: 109-151.

de Bernardi, G., and R. Giussani. 1990. Are blue-green algae a suitable food for zooplankton? An overview. Hydrobiologia 200-201: 29-41.

Denman, K.L., and A.E. Gargett. 1983. Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean. Limnol. Oceanogr. 28: 801-815.

Dower, J.F., T.J. Miller, and W.C. Leggett. 1997. The role of microscale turbulence in the feeding ecology of larval fish, p. 169-220. *In* J.H.S. Blaxter and A.J. Southward [eds.], Advances in Marine Biology, Vol. 31. Academic Press.

Dower, J.F., P. Pepin, and W.C. Leggett. 1998. Enhanced gut fullness and an apparent shift in size selectivity by radiated shanny (*Ulvaria subbifurcata*) larvae in response to increased turbulence. Can. J. Fish. Aquat. Sci 55: 128-142.

Drenner, .W., J. . Strickler, and W.J. O'Brien. 1978. Capture probability: the role of zooplankter escape in the selective feeding of planktivorous fish. J. Fish Res. Board Can. 35: 1370-1373.

Dunson, W.A., and J. Travis. 1991. The role of abiotic factors in community organization. Am. Nat. 138: 1067-1091.

Eiane, K., D.L. Aksnes, and J. Giske. 1997. The significance of optical properties in competition among visual and tactile predators: A theoretical study. Ecol. Model. 98: 123-136.

Eie, A.J., and R. Borgstrøm. 1981. Distribution and food of roach (*Rutilus rutilus* (L.) and perch (*Perca fluviatilis* L.) in the eutrophic lake Årungen, Norway. Verh. Internat. Verein. Limnol. 21: 1257-1263.

Eloranta, P. 1978. Light penetration in different types of lakes in Central Finland. Holarct. Ecol. 1: 362-366.

Elser, M.M., C.N. von Ende, P. Sorrano, and S.R. Carpenter. 1987. *Chaoborus* populations: response to food web manipulation and potential effects on zooplankton communities. Can. J. Zoolog. 65: 2846-2852.

Estlander, S., L. Nurminen, M. Olin, M. Vinni, and J. Horppila. 2009. Seasonal fluctuations in macrophyte cover and water transparency of four brown-water lakes: implications for crustacean zooplankton in littoral and pelagic habitats. Hydrobiologia 620: 109-120.

Etemad-Shahidi, A. and J. Imberger. 2001. Anatomy of turbulence in thermally stratified lakes. Limnol. Oceanogr. 46: 1158-1170.

Evans, R.D. 1994. Empirical evidence of the importance of sediment resuspension in lakes. Hydrobiologia 284: 5-12.

Evans, C.D., D.T. Monteith, and D.M. Cooper. 2005. Long-term increases in surface water dissolved organic carbon: Observations, possible causes and environmental impacts. Environ. Pollut. 137: 55-71.

Fields, J.M., and J. Yen. 2002. Fluid mechanosensory stimulation of behaviour from a planktonic marine copepod, *Euchaeta rimana* Bradford. J. Plankton Res. 24: 747-755.

Finnish Standard Association. 1993. Determination of chlorophyll a in water. Extraction with ethanol. Standard 5772. Helsinki.

Frey, K.E., and L. Smith. 2005. Amplified carbon release from vast west Siberian peatlands by 2100. Geophys. Res. Lett. 32: L09401, doi:10.1029/2004GL022025

G.-Tóth, L., L. Parpala, C. Balogh, I. Tátrai, and E. Baranyai. 2011. Zooplankton community response to enhanced turbulence generated by water-level decrease in Lake Balaton, the largest shallow lake in Central Europe. Limnol. Oceanogr. 56: 2211-2222.

George, G. [ed.]. 2010. The Impact of Climate Change on European Lakes. Springer, Dordrecht.

Gerritsen, J., and R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Board Can. 34: 73-82.

Giorgi, F., X. Bi, and J. Pal. 2004. Mean, interannual variability and trends in a regional climate change experiment over Europe. II: climate change scenarios (2071-2100).

Gliwicz, Z.M., K. Biernacka, J. Pijanowska, and R. Korsak. 2000. Ontogenetic shifts in the migratory behavior of *Chaoborus flavicans* Meigen: Field and experimental evidence. Arch. Hydrobiol. 149: 193-212.

Granéli, W. 2012. Brownification of lakes, p. 117-119. *In* L. Bengtsson, R. Herschy and R. Fairbridge [eds.], Encyclopedia of Lakes and Reservoirs. Springer Science.

Guthrie, D.M., and W.R.A. Muntz. 1993. Role of vision in fish behaviour. Fish. Fisheries Serie. 7: 89–128.

Haertel, S. S. and R. Eckmann. 2002. Diel diet shift of roach and its implications for the estimation of daily rations. J. Fish. Biol. 60: 876-892.

Hagman, A.-E., K. Serenius, and S. Rajajärvi. 2008. Mäntsälän järvien kunnostuksen yleissuunnitelma. Uudenmaan ympäristökeskuksen raportteja 3. (In Finnish)

Hinshaw, J.M. 1985. Effects of illumination and prey contrast on survival and growth of larval Yellow perch (*Perca flavescens*). T. Am. Fish. Soc. 114: 540-545.

Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91: 293-320.

Holt, R.D., and G.A. Polis. 1997. A theoretical framework for intraguild predation. Am. Nat. 149: 745-764.

Hongve, D., G. Riise, and J.F. Kristiansen. 2004. Increased colour and organic acid concentrations in Norwegian forest lakes and drinking water – a result of increased precipitation? Aquat. Sci. 66: 231-238.

Horppila, J., and L. Nurminen. 2003. Effects of submerged macrophytes on sediment resuspension and internal phosphorus loading in Lake Hiidenvesi (southern Finland). Wat. Res. 37: 4468-4474.

Horppila, J. and A. Liljendahl-Nurminen. 2005. Clay-turbid interactions may not cascade - a reminder for lake managers. Restor. Ecol. 13: 241-245.

Horppila, J., S. Estlander, M. Olin, J. Pihlajamaki, M. Vinni, and L. Nurminen. 2011. Gender-dependent effects of water quality and conspecific density on the feeding rate of fish - factors behind sexual growth dimorphism. Oikos 120: 855–861.

Horppila, J., A. Liljendahl-Nurminen, and T. Malinen. 2004. Effects of clay turbidity and light on the predator-prey interaction between smelts and chaoborids. Can. J. Fish Aquat. Sci. 61: 1862-1870.

Horppila, J, M. Olin, M. Vinni, S. Estlander, L. Nurminen, M. Rask, J. Ruuhijärvi, and H. Lehtonen. 2010. Perch production in forest lakes: the contribution of abiotic and biotic factors. Ecol. Freshw. Fish 19: 257–266.

Horridge, G.A. 1966. Some recently discovered underwater vibration receptors in invertebrates, p. 395-405. *In* H. Barnes [ed.], Some contemporary studies in marine science. Allen and Undwin.

Hrbáček, J., B. Draková, V. Korínek, and L. Procházková. 1961. Demonstration of the effects of fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton assosiation. Verh. Internat. Verein. Limnol. 14: 192-195.

Huisman, J., J. Sharples, J.M. Stroom, P.M. Visser, W.E.A. Kardinaal, J.M.H. Verspagen, and B. Sommeijer. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology 85: 2960-2970.

Hutchinson, G.E. 1961. The paradox of plankton. Am. Nat. 95: 137-145.

Imboden, D.M., and A. Wüest. 1995. Mixing mechanisms in lakes, p. 83-138. *In* A. Lerman, D. Imboden and J. Gat [eds.], Physics and chemistry of lakes, 2nd ed. Springer-Verlag Berlin Heidelberg New York.

IPCC. 2001. Climate Change 2001: Impacts, Adaptation & Vulnerability: Contribution of Working Group II to the Third Assessment Report of the IPCC. *In* J.J. McCarthy, O.F. Canziani, N.A. Leary, D.J. Dokken and K.S. White [eds.]. Cambridge, UK, Cambridge University Press. 1000 pp.

Irigoien, X., R.P. Harris, and R.N. Head. 2000. Does turbulence play a role in feeding and reproduction of *Calanus finmarchicus*. J. Plankton Res. 22: 399-407.

Iversen, K.R., R. Primicerio, A. Larsen, J.K. Egge, F. Peters, Ó. Guadayol, A. Jacobsen, H. Havskum, and C. Marrasé. 2010. Effects of small-scale turbulence on lower trophic levels under different nutrient conditions. J. Plankton Res. 32: 197-208.

Jones, R.I. 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia 229: 73-91.

Karlsson, J., P. Byström, J. Ask, P. Ask, L. Persson, and M. Jansson. 2009. Light limitation of nutrient-poor lake ecosystems. Nature 460: 506-509.

Kerfoot, W. C. (1975). The divergence of adjacent populations. Ecology 56: 1298-1313.

Kiørboe, T. and E. Saiz, 1995. Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. Mar. Ecol.-Proc. Ser. 122: 135-145.

Kirk, J.T.O. 1994. Light & photosynthesis in aquatic ecosystems, 2nd ed. Cambridge University Press, Cambridge, United Kingdom.

Koroleff, F. 1979. Methods for the chemical analysis for seawater. Meri 7: 1–60.

Kortelainen, P. 1993. Content of total organic carbon in Finnish lakes and its relationship to catchment characteristics. Can. J. Fish. Aquat. Sci. 50: 1477-1483.

Lagadeuc, Y., M. Bouté, and J.J. Dodson. 1997. Effect of vertical mixing on the vertical distribution of copepods in coastal waters. J. Plankton Res. 19: 1183-1204.

Lammens, E.H.R.R., J. Geursen, and P.J. MacGillavry. 1987. Diet shifts, feeding efficiency, and coexistence of bream (*Abramis brama*), roach (*Rutilus rutilus*) and white bream (*Blicca bjoerkna*) in hypertrophic lakes. Proc. V. Congr. Europ. Ichtyol. Stockholm 1985: 153-162.

Lampert, W. 1987. Predictability in lake ecosystems: the role of biotic interactions, p. 333-345. *In* E.D. Schultze, and H. Zwölfer, [eds.], Potentials and limitations of ecosystem analysis. Ecological Studies 61. Springer-Verlag, Heidelberg.

Lampert, W. 1993. Ultimate causes of diel vertical migration of zooplankton: New evidence for the predator avoidance hypothesis. Arch. Hydrobiol. Beih. Ergebn. Limnol. 39: 79–88.

Lampert, W., Fleckner, W., Rai, H. and Taylor, B.E. (1986). Phytoplankton control by grazing zooplankton: A study on the spring clear-water phase. Limnol. Oceanogr. 31: 478-490.

Ledbetter, M. 1979. Langmuir circulations and plankton patchiness. Ecol. Model. 7: 289-310.

Lee, C.-H, H.-U. Dahms, S.-H. Cheng, S. Souissi, F.G. Schmitt, R. Kumar, and J.-S. Hwang. 2010. Predation of *Pseudodiaptomus annandalei* (Copepoda: Calanoida) by the grouper fish *Epinephelus coioides* under different hydrodynamic conditions. J. Exp. Mar. Biol. Ecol. 393: 17-22.

Lehman, J.T. and C.D. Sandgren. 1985. Species specific rates of growth and grazing loss among freshwater algae. Limnol. Oceanogr. 30: 34-46.

Lévesque, S., B.E. Beisner and P.R. Peres-Neto. 2010. Meso-scale distributions of lake zooplankton reveal spatially and temporally varying trophic-cascades. J. Plankton Res. 32: 1369-1384.

Liljendahl-Nurminen, A., J. Horppila, T. Malinen, P. Eloranta, M. Vinni, E. Alajärvi, and S. Valtonen. 2003. The supremacy of invertebrate predators over planktivorous fish – factors behind the unconventional seasonal dynamics of cladocerans in Lake Hiidenvesi. Arch. Hydrobiol. 158: 75-96.

Liljendahl-Nurminen, A., J. Horppila, and W. Lampert. 2008. Physiological and visual refuges in a metalimnion: an experimental study of effects of clay-turbidity and an oxygen minimum on fish predation. Freshw. Biol. 53: 945-951.

Lind, O.T. 200 . Suspended clay's effect on lake and reservoir limnology. Arch. Hydrobiol. Suppl. 139: 327-360.

Luecke, C. 1986. A change in the pattern of vertical migration of *Chaoborus flavicans* after the introduction of trout. J. Plankton Res. 8: 649-657.

Maar, M., T.G. Nielsen, A. Stips, and A.W. Visser. 2003. Microscale Distribution of Zooplankton in Relation to Turbulent Diffusion. Limnol. Oceanogr. 48: 1312-1325.

MacIntyre, S. 1993. Vertical mixing in a shallow, eutrophic lake: possible consequences for the light climate of phytoplankton. Limnol. Oceanogr. 38: 798-817.

MacKenzie, B.R., and T. Kiørboe. 2000. Larval fish feeding and turbulence: A case for the downside. Limnol. Oceanogr. 45: 1-10.

MacKenzie, B.R., and W.C. Leggett. 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. Mar. Ecol.-Prog. Ser. 73: 149-160.

MacKenzie, B.R., T.J. Miller, S. Cyr, and W.C. Leggett. 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. Limnol. Oceanogr. 39: 1790-1799.

Malinen, T., J. Horppila, and A. Liljendahl-Nurminen. 2001. Langmuir circulations disturb the low-oxygen refuge of phantom midge larvae. Limnol. Oceanogr. 46: 689-692.

Malinen, T., A. Tuomaala and H. Peltonen. 2005. Vertical and horizontal distribution of smelt (*Osmerus eperlanus*) and implications of distribution patterns for stock assessment. Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 59: 141–159.

Marrasé, C., J.H. Costello, T. Granata, and J.R. Strickler. 1990. Grazing in a turbulent environment: Energy dissipation, encounter rates, and efficacy of feeding currents in *Centropages hamatus*. P. Natl. Acad. Sci USA 87: 1653-1657.

McQueen, D.J., J.R. Post, and E.L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Can. J. Fish. Aquat. Sci. 43: 1571-1581.

Meager, J.J., T. Solbakken, A.C. Utne-Palm, and T. Oen. 2005. Effects of turbidity on the reactive distance, search time, and foraging success of juvenile Atlantic cod (*Gadus morhua*). Can. J. Fish Aquat. Sci. 62: 1978-1984.

Metcalfe, A.M., T.J. Pedley, and T.F. Thingstad. 2004. Incorporating turbulence into a plankton foodweb model. J. Marine Sys. 49: 105-122.

Moeseneder, M.M. and G.J. Herndl. 1995. Influence of turbulence on bacterial production in the sea. Limnol. Oceanogr. 40: 1466-1473.

Mooij, W.M., S. Hülsmann, L.N. De Senerpont Domis, B.A. Nolet, P.L.E. Bodelier, P.C.M Boers, L. Miguel Dionisio Pires, H.J. Gons, B.W. Ibelings, R. Noordhuis, R. Portielje, K. Wolfstein, and E.H.R.R. Lammens. 2005. The impact of climate change on lakes in the Netherlands: a review. Aquat. Ecol. 39: 381-400.

Nicolle, A., L.-A. Hansson, J. Brodersen, P.A. Nilsson, and C. Brönmark. 2011. Interactions between predation and resources shape zooplankton population dynamics. PLoS ONE 6: e16534, doi:10.1371/journal.pone.0016534

Nordbo, A., S. Launiainen, I. Mammarella, M. Leppäranta, J. Huotari, A. Ojala, and T. Vesala. 2011. Long-term energy flux measurements and energy balance over a small boreal lake using eddy covariance technique. J. Geophys. Res. 116: D02119, doi: 10.1029/2010JD014542

Nurminen, L., J. Horppila, and Z. Pekcan-Hekim. 2007. Effect of light and predator abundance on the habitat choice of plant-attached zooplankton. Freshw. Biol. 52: 539-548.

O'Bryan, L.M., and G.E. Forrester. 1997. Effects of fish presence and simulated moonlight gradients on night-time horizontal movements of a predatory zooplankter, *Chaoborus punctipennis*. J. Plankton Res. 19: 1441-1453.

Osborn, T., and A. Scotti. 1996. Effect of turbulence on predator-prey contact rates: where do we go from here? Mar. Ecol.-Prog. Ser. 139: 302-304.

Pace, M.L., J.J. Cole, S.R. Carpenter, and J.F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends Ecol. 14: 483-488.

Pace, M.L. and J.J. Cole. 2002. Synchronous variation of dissolved organic carbon and color in lakes. Limnol. Oceanogr. 47: 333-342.

Packard, A.T. 2001. Clearance rates and prey selectivity of the predaceous cladoceran *Polyphemus pediculus*. Hydrobiologia 442: 177-184.

Parma, S. 1971. *Chaoborus flavicans* (Meigen)(Diptera, Chaoboridae): an autecological study. PhD Thesis, Rijksuniversiteit te Groningen, Germany.

Pastorok, R.A. 1980. The effects of predator hunger and food abundance on prey selection by *Chaoborus* larvae. Limnol. Oceanogr. 25: 910-921.

Pastorok, R.A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. Ecology 62: 1311-1324.

Pécseli, H.L., J.K. Trulsen and Ø. Fiksen. 2010. Predator–prey encounter rates in turbulent water: Analytical models and numerical tests. Prog. Oceanogr. 85: 171-179.

Pekcan-Hekim, Z., and J. Lappalainen. 2006. Effects of clay turbidity and density of pikeperch (Snader lucioperca) larvae on predation by perch (Perca fluviatilis). Naturwissenschaften 93: 356-359.

Pekcan-Hekim, Z., J. Horppila, L. Nurminen, and J. Niemistö. 2005. Diel changes in habitat preference and diet of perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and white bream (*Abramis björkna*). Arch. Hydrobiol. Spec. Issues Adv. Limnol. 59: 173-187.

Peters, F., C. Marrasé, H. Havskum, F. Rassoulzadegan, J. Dolan, M. Alcaraz, and J.M. Gasol. 2002. Turbulence and the microbial food web: effects on bacterial losses to predation and on community structure. J. Plankton Res. 24: 321-331.

Pope, G.F., J.C.H. Carter, and G. Power. 1973. The influence of fish on the distribution of *Chaoborus* spp. (Diptera) and density of larvae in Matamek River System. T. Am. Fish. Soc. 102: 707-722.

Preusse M., F. Peeters and A. Lorke. 2010. Internal waves and the generation of turbulence in the thermocline of a large lake. Limnol. Oceanogr. 55: 2353-2365.

Pryor S.C., R.J. Barthelmie, and E. Kjellström. 2005. Potential climate change impact on wind energy resources in northern Europe: analysis using a regional climate model. Clim. Dynam. 25: 815-835.

Rahel F.J., and J.W. Nutzman. 1994. Foraging in a lethal environment: fish predation in hypoxic waters of a stratified lake. Ecology 75: 1246–1253.

Ramcharan, C.W., D.J. McQueen, A. Pérez-Fuentetaja, N. D. Yan, E. Demers, and J. Rusak. 2001. Complex responses of *Chaoborus* to changes in fish populations. Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 56: 81-100.

Ranåker, L., M. Jönsson, P.A. Nilsson, C. Brönmark. 2012. Effects of brown and turbid water on piscivore–prey fish interactions along a visibility gradient. Freshw. Biol. 57: 1761-1768.

Rask, M., M. Viljanen, and J. Sarvala. 1999. Humic lakes as fish habitats, p. 209–224. *In* J. Keskitalo, and P. Eloranta [eds.], Limnology of humic waters. Leiden, Backhuys Publishers.

Read, J.S., D.P. Hamilton, A.R. Desai, K.C. Rose, S. MacIntyre, J.D. Lenters, R.L. Smyth, P.C. Hanson, J.J. Cole, P.A. Staehr, J.A. Rusak, D.C. Pierson, J.D. Brookes, A. Laas, and C.H. Wu. 2012. Lake-size dependency of wind shear and convection as controls on gas exchange. Geophys. Res. Lett. 39: L09405, doi: 10.1029/2012GL051886

Richmond, H.E., T.R. Hrabik, and A.F. Mensinger. 2004. Light intensity, prey detection and foraging machanisms of age 0 year yellow perch. J. Fish Biol. 65: 195-205.

Riessen, H.P., W.J. O'Brien, and B. Loveless. 1984. An analysis of the components of *Chaoborus* predation on zooplankton and the calculation of relative prey vulnerabilities. Ecology 65: 514-522.

Riessen, H.P., J.W. Sommerville, C. Chiappari, and D. Gustafson. 1988. *Chaoborus* Predation, Prey Vulnerability, and their Effect in Zooplankton Communities. Can. J. Fish. Aquat. Sci 45: 1912-1920.

Rothschild, B.J., and T.R. Osborn. 1988. Small-scale turbulence and plankton contact rates. J. Plankton Res. 10: 465-474.

Roulet, N., and T.R. Moore. 2006. Environmental chemistry - Browning the waters. Nature 444: 283-284.

Saggio, A., and J. Imberger. 2001. Mixing and turbulent fluxes in the metalimnion of a stratified lake. Limnol. Oceanogr. 46: 392-409.

Saiz E., and M. Alcaraz. 1992. Free-swimming behavior of *Acartia clausi* (Copepoda: Calanoida) under turbulent water movement. Mar. Ecol. Prog.-Ser. 80: 229–236.

Saiz, E., and T. Kiørboe. 1995. Predatory and suspension-feeding of the copepod *Acartia tonsa* in turbulent environments. Mar. Ecol.-Prog. Ser. 122: 280-289.

Saiz, E., M. Alcaraz, and G.-A. Paffenhöfer. 1992. Effects of small-scale turbulence on feeding rate and gross-growth efficiency of three *Acartia* species (Copepoda: Calanoida). J. Plankton Res. 14: 1085-1097.

Samuelsson, P. 2010. Using regional climate models to quantify the impact of climate change on lakes, p. 15-32. *In* G. George [ed]. The impact of climate change on European lakes. Dordrecht, Springer.

Sandström, A. 1999. Visual ecology of fish – a review with special reference to percids. Fiskeriverket Rapport 2: 45-80.

Sarvala, J., P. Kankaala, P. Zingel, and L. Arvola. 1999. Zooplankton, p. 173–191. *In* J. Keskitalo, and P. Eloranta [eds.], Limnology of humic waters. Leiden, Backhuys Publishers.

Seuront L., H. Yamazaki, and S. Souissi. 2004. Hydrodynamic disturbance and zooplankton swimming behaviour. Zool. Stud. 43: 376-387.

Scheffer, M. 1998. Ecology of shallow lakes. Chapman and Hall, London.

Sluss, T.D., G.A. Cobbs, and J.H. Thorp. 2008. Impact of turbulence on riverine zooplankton: a mesocosms experiment. Freshw. Biol. 53: 1999-2010.

Smyly, W.J.P. 1980. Food and feeding of aquatic larvae of the midge *Chaoborus flavicans* (Meigen)(Diptera: Chaoboridae) in the laboratory. Hydrobiologia 70: 179-188.

Snickars, M., A. Sandström and J. Mattila. 2004. Antipredator behaviour of 0+ year *Perca fluviatilis*: effect of vegetation density and turbidity. J. Fish Biol. 65: 1604-1613.

Sobek, S., L.J. Tranvik, Y.T. Prairie, P. Kortelainen, and J.J. Cole. 2007. Patterns and regulation of dissolved organic carbon: An analysis of 7,500 widely distributed lakes. Limnol. Oceanogr. 52: 1208-1219.

Sommer, U., F. Sommer, B. Santer, C. Jamieson, M. Boersma, C. Becker, and T. Hanse. 2001. Complementary impact of copepods and cladocerans on phytoplankton. Ecol. Lett. 4: 545-550.

Šorf, M., Z. Brandl, P. Znachor, and M. Vašek. 2014. Different effects of planktonic invertebrate predators and fish on the plankton community in experimental mesocosms. Ann. Limnol. – Int. J. Lim. 50: 71-83.

Steiner, C.F. 2001. The effects of prey heterogeneity and consumer identity on the limitation of trophic-level biomass. Ecology 82: 2495-2506.

Stenson, J.A.E. 1980. Predation pressure from fish and two *Chaoborus* species as related to their visibility, p. 618-622. *In* C. Kerfoot [ed.], Evolution and ecology of zooplankton communities. American Society of Limnol. Oceanogr. Special Symposium 3, Univ. Press of New England, Hanover.

Stenson, J.A.E. 1990. Creating conditions for changes in prey community structure by *Chaoborus* spp. in a lake in Sweden. Hydrobiologia, 198, 205-214.

Suikkanen, S., S. Pulina, J. Engström-Öst, M. Lehtiniemi, S. Lehtinen, and A. Brutemark. 2013. Climate change and eutrophication induced shifts in northern summer plankton communities. PLoS ONE 8: e66475, doi: 10.1371/journal.pone.0066475

Sundby, S. and P. Fossum. 1990. Feeding conditions of Arcto-norwegian cod larvae compared with the Rothschild–Osborn theory on small-scale turbulence and plankton contact rates. J. Plankton Res. 12: 1153-1162.

Swift, M.C., and A.Y. Fedorenko. 1973. A rapid method for the analysis of the crop contents of *Chaoborus* larvae. Limnol. Oceanogr. 18: 795-798.

Swift, M.C., and A.Y. Fedorenko. 1975. Some aspects of prey capture by *Chaoborus* larvae. Limnol. Oceanogr. 20: 418-425.

Tennekes, H., J.I. Lumley. 1972. A First Course in Turbulence. MIT Press, Cambridge, Massachusetts.

Teraguchi, M., and T.G. Northcote. 1966. Vertical distribution and migration of *Chaoborus flavicans* larvae in Corbett Lake, British Columbia. Limnol. Oceanogr. 11: 164-176.

ter Braak, C.J.F., and C.W.N. Looman. 1994. Biplots in reduced-rank regression. Biometrical J. 36: 983-1003.

ter Braak, C.J.F., and P. Šmilauer. 2002. CA OCO eference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Microcomputer Power, Ithaca, NY, USA.

Thingstad, T.F., and R. Lignell. 1997. Theoretical models for the control of bacterial growth rate, abundance, diversity and carbon demand. Aquat. Microb. Ecol. 13: 19–27.

Thomas, W.T., and C.H. Gibson. 1990. Effects of small-scale turbulence on microalgae. J. Appl. Phycol. 2: 71-77.

Thorpe, S.A. 2004. Langmuir circulation. Annu. Rev. Fluid. Mech. 36: 55-79.

Thorpe, S.A., T.R. Osborn, D.M. Farmer, and S. Vagle. 2003. Bubble clouds and Langmuir Circulation: Observations and Models. J. Phys. Oceanogr. 33: 2013-2031.

Tolonen, K.T., J. Karjalainen, S. Staff, and M. Leppä. 2000. Individual and population-level food consumption by cyprinids and percids in a mesotrophic lake. Ecol. Freshw. Fish 9: 153-162.

Utne-Palm, A.C. 2002. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. Mar. Freshw. Behav. Physiol. 35: 111-128.

Vanni, M.J., and D.L.Finlay. 1990. Trophic cascades and phytoplankton community structure. Ecology 71: 921-937.

Vanni, M.J., C. Luecke, J.F. Kitchell, Y. Allen, J. Temte, and J.J. Magnuson. 1990. Effects on lower trophic levels of massive fish mortality. Nature 344: 333-335.

Vinyard, G.L. and W.J. O'Brien. 1976. ff ects of light and turbidity on the reaction distance of Bluegill (*Lepomis macrochirus*). J. Fish. Res. Board. Can. 33: 2845-2849.

von Ende, C.N. 1979. Fish predation, interspecific predation, and the distribution of two *Chaoborus* species. Ecology 60: 119-128.

von Ende, C.N. and D.O. Dempsey. 1981. Apparent exclusion of the cladoceran *Bosmina longirostis* by invertebrate predator *Chaoborus americanus*. Am. Nat. 105: 240-248.

Voss S. and H. Mumm. 1999. Where to stay by night and day: Size-specific and seasonal differences in horizontal and vertical distribution of *Chaoborus flavicans* larvae. Freshw. Biol. 42: 201-213.

Wagner-Döbler, I. 1988. Vertical migration of *Chaoborus flavicans* (Diptera, Chaoboridae): The control of day and night depth by environmental parameters. Arch. Hydrobiol. 114: 251-274.

Wissel, B. and J. Benndorf. 1998. Contrasting effects of the invertebrate predator *Chaoborus obscuripes* and planktivorous fish on plankton communities of a long term biomanipulation experiment. Arch. Hydrobiol. 143: 129-146.

Wissel, B., W.J. Boeing, and C.W. Ramchran. 2003. Effects of water color on predation regimes and zooplankton assemblages in freshwater lakes. Limnol. Oceanogr. 48: 1965-1976.

Wrona, F.J., T.D. Prowse, J.D. Reist, H.E. Hobbie, L.M.J. Levesqué, and W.F. Vincent. 2006. Climate change effects of aquatic biota, ecosystem structure and function. Ambio 35: 359-369.

Yen, J. and J.R. Strickler. 1996. Advertisement and concealment in the plankton: what makes a copepod hydrodynamically conspicuous? Invertebr. Biol. 115: 191-205.

Zaret, T.M. 1980. Predation and freshwater communities. Yale University Press, New Haven.