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Effects of turbidity on feeding and distribution of fish

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Academic dissertation

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Camgöz'le Sardalya

*Gelelim balıkların öyküsüne,
Camgöz balığını bilir misiniz?
Köpek balığından biraz küçük bir deniz canavarı.
Sardalya balıklarına bayılmış.
Sardalya balıkları, camgözün yaklaşmakta olduğunu
kokusundan mı, denizin kıpırtısından mı nasılsa
anlarlar, hemen bir araya gelir, birleşir, yanyana,
sırt sırta bir duvar oluştururlarmış.*

*Camgöz gelir, gelir, gelir, iyice sokuldu mu,
sardalya balıkları birden pullarını silkeleyip
kaçarlarmış. Sonra bu pullar denizin üzerinde
pırıldamaya başladı mı balıkçılar, burada camgöz
var deyip, ağlarını atar, kazıklarını çakarlarmış.*

*(Aziz Nesin'in Büyükler İçin Masallar adlı kitabından)
Ruhi Su Türküsü*

Cow Shark and Sardine

*Let's get to the story of the fish
Do you know a fish named "cow shark"?
A small shark and a sea monster
It loves eating sardines*

*Sardines, could be the smell or the movement of the sea, would sense the approach of the cow shark
So they would gather together and line up side-by-side to form a wall with their backs*

*The Cow shark would get closer, closer, and when it is really close
Sardines would shake, let their scales scatter to the water
And escape
Then when these scales would start sparkling on the sea surface
The fishermen would know there is cow shark in here
And start throwing their nets, driving their stakes*

*(Adapted from "Fairy Tales for Grown-Ups" by Aziz Nesin)
Ruhi Su Turkish Folk Song*

Abstract

In aquatic systems, the ability of both the predator and prey to detect each other may be impaired by turbidity. This could lead to significant changes in the trophic interactions in the food web of lakes. Most fish use their vision for predation and the location of prey can be highly influenced by light level and the clarity of the water environment. Turbidity is an optical property of water that causes light to be scattered and absorbed by particles and molecules. Turbidity is highly variable in lakes, due to seasonal changes in suspended sediments, algal blooms and wind-driven suspension of sediments especially in shallow waters. There is evidence that human activity has increased erosion leading to increased turbidity in aquatic systems. Turbidity could also play a significant role in the distribution of fish. Turbidity could act as a cover for small fish and reduce predation risk. Diel horizontal migration by fish is common in shallow lakes and is considered a consequence of either optimal foraging behaviour or a trade-off between foraging and predator avoidance. In turbid lakes, diel horizontal migration patterns could differ since turbidity can act as a refuge and affect the predator-prey interactions.

Laboratory experiments were conducted with perch (*Perca fluviatilis* (L.)) and white bream (*Abramis björkna* (L.)) to clarify the effects of turbidity on their feeding. Additionally, to clarify the effects of turbidity on predator preying on different types of prey, pikeperch larvae (*Sander lucioperca* (L.)), *Daphnia pulex* (Leydig), *Sida crystallina* (O.F. Müller), and *Chaoborus flavicans* (Meigen) were used as prey in different experiments. To clarify the role of turbidity in the distribution and diel horizontal migration of perch, roach (*Rutilus rutilus* (L.)) and white bream, field studies were conducted in shallow turbid lakes. A clear and a turbid shallow lake were compared to investigate the distribution of perch and roach in these two lakes over a 15 year study period.

The feeding efficiency of perch and white bream was not significantly affected with increasing clay turbidity up to 50 NTU. The perch experiments with pikeperch larvae suggested that clay turbidity could act as a refuge especially at turbidity levels higher than 50 NTU. Perch experiments with different prey types suggested that pikeperch larvae are probably better at using turbidity as a refuge compared to *Daphnia*. Increase in turbidity probably has a stronger effect on perch preying on plant-attached prey.

The main findings of this thesis show that turbidity can play a significant role in the distribution of fish. Perch and roach could use turbidity as refuge when macrophytes disappear while small perch may also use high turbidity as refuge when macrophytes are present. Floating-leaved macrophytes probably provide good refuge for small fish in clay-turbid lakes and provide a certain level of turbidity and not too complex structure for refuge. The results give light to the predator-prey interactions in turbid environments. The turbidity of water should be taken into account when studying the diel horizontal migrations and distribution of fish in shallow lakes.

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List of original publications

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

- I** Pekcan-Hekim Z. and Lappalainen J. 2006. Effects of clay turbidity and density of pikeperch (*Sander lucioperca*) larvae on predation by perch (*Perca fluviatilis*). *Naturwissenschaften* 93, 356-359.
- II** Nurminen L., Pekcan-Hekim Z., Horppila J. and Repka S. Haven in the mist – Does turbidity affect the importance of habitat as refuge? *Submitted manuscript*.
- III** Pekcan-Hekim Z. and Horppila J. 2007. Feeding efficiency of white bream at different inorganic turbidities and light climates. *Journal of Fish Biology* 70, 474-482.
- IV** Pekcan-Hekim Z., Horppila J., Nurminen L. and Niemistö J. 2005. Diel changes in habitat preference and diet of perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and white bream (*Abramis björkna*). *Archiv für Hydrobiologie Special Issues Advances in Limnology* 59, 173-187.
- V** Pekcan-Hekim Z., Horppila J., Nurminen L. Ojala T., Olin M. and Ruuhijärvi J. Diurnal habitat shifts of planktivorous perch in a shallow lake – the effects of structural complexity, turbidity and food availability. *Submitted manuscript*.
- VI** Pekcan-Hekim Z., Pedersen A. R., Kristensen T.B., Lauridsen T. L., Søndergaard M. and Jeppesen E. Spatial distribution of roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in two shallow lakes subjected to changes in trophic state during a 15 year study. *Manuscript*.

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1. Introduction

1.1 Role of fish as predators in lakes

Predator-prey interactions have a major role in shaping the food-web structures of lakes (Sih et al. 1985, Lima & Dill 1990). Predation by top predators can have significant effects on species lower down in the food web (Paine 1980, Carpenter & Kitchell 1993). The importance of fish as predators in lakes is that they may significantly affect species composition and biomass at other trophic levels (Kerfoot & Sih 1987). The effects of predation by fish can be exerted on lower trophic levels directly (O'Brien 1987a) and indirectly (Miller & Kerfoot 1987, Romare & Hansson 2003). The direct effect of fish can be through consumption leading to reduced prey density (Mills et al. 1987). The indirect effect of predation is defined as the effect that modifies the direct effect of one species on another (Miller & Kerfoot 1987). Indirect effects of predation may be divided into trophic linkage, behavioural and chemical responses that follow different pathways and function through different mechanisms. An example of trophic linkage indirect effects could be the top-down regulation of phytoplankton, through decreasing fish predation that leads to increased zooplankton grazing (Carpenter et al. 1985). Behavioural indirect effects of fish predation can be by influencing the behaviour of prey (Mittelbach 1984, Mittelbach & Chesson 1987). The presence of predators may alter the behaviour of prey making them more difficult to capture, detect or encounter. Reduced activity, swarming and hiding of prey are responses observed in the presence of predators (Lima & Dill 1990, Lindén et al. 2003, Lehtiniemi & Lindén 2006). Behavioural indirect effects of predation usually involve a response of movement to different habitats (Werner et al. 1983). The response of prey to predation risk, such as movement to refuges or different habitats, may cause significant changes in food web linkages (Lima 1998, Sih et al. 1998, Persson 1999). Lake morphometry

is also of importance in predator-prey interactions. Jeppesen et al. (1997) showed that predatory control by fish is more important in shallow lakes than in deep lakes. This was suggested because of the higher fish biomass per unit of volume in shallow lakes. Additionally, zooplankton may have a lower chance of avoiding fish predation in shallow lakes (Jeppesen et al. 1997).

Most fish use their vision for predation (Guthrie & Muntz 1993). The process of predation includes the following steps; location of prey, pursuit, attack and retention (O'Brien 1987a, Clarke et al. 2005). For predators that use visual stimulus, the location of prey can be highly influenced by the light level and the clarity of the water environment (Vinyard & O'Brien 1976, O'Brien 1987a, Utne-Palm 1999). Hence, in aquatic systems, the ability of both the predator and the prey to detect each other may be impaired by turbidity (Abrahams & Kattenfeld 1997). Predation pressure is suggested to be low in eutrophic and turbid lakes since turbidity may offer zooplankton refuge from visually hunting fish predators (Jeppesen 1998).

1.2 Sources and types of turbidity

Turbidity is highly variable in nature due to seasonal changes in suspended sediments, algal blooms and wind-driven suspension of sediments in shallow waters (Weyhenmeyer et al. 1996, Scheffer 1998). Turbidity can also vary spatially within a lake (Scheffer et al. 1994, Niemistö et al. 2005). The suspended particles in the water can be clay, silt, finely divided inorganic and organic matter that can arise from erosion, decomposition of rocks, soil and dead plant material (Bruton 1985). With snow and rainfall organic matter, soil and particles are washed into rivers, lakes and coastal areas of the sea causing turbidity (Bruton 1985). There is evidence that human activity has increased erosion leading to an increase in turbidity in aquatic systems (Beeton 2002). The increase in turbidity can have considerable impacts on lake ecosystems by influencing nutrient fluxes, primary

production, the feeding of herbivorous zooplankton and fish (Gliwicz & Rybak 1976, Bruton 1985, Dillon et al. 1990, Kirk & Gilbert 1990, Hellström 1991, Lind 2003). Bruton (1985) stated that turbidity can have major ecological impacts on primary productivity and trophic status by reducing the depth of the photosynthetic zone. Furthermore, turbidity plays an important role on predator-prey interactions that control trophic status in aquatic systems.

Turbidity is an optical property of water that causes light to be scattered and absorbed by particles and molecules (Kirk 1981). In lakes, both organic and inorganic matter can cause turbidity. Phytoplankton turbidity is an example of turbidity caused by organic matter. Inorganic suspendoids such as clay can cause turbidity moreover affect the primary production by reducing the available light photons for phytoplankton and macrophytes (Lind 2003). In clay-turbid lakes, turbidity is mainly caused by inorganic particles eroded from drainage areas or suspended from sediment (Nolen et al. 1985, Niemistö et al. 2005). Strong winds can mix the water column and create turbidity especially in shallow lakes (Scheffer 1998). Benthivorous fish can also contribute to turbidity by stirring the sediment while feeding (Parkos et al. 2003, Scheffer et al. 2003).

In this thesis clay turbidity is used in the experiments conducted in articles **I**, **II** & **III** and the field data were obtained from lakes where the main cause of turbidity is clay (**IV** & **V**). In article **VI** the data were collected from two lakes with phytoplankton turbidity. The reliable measure of turbidity has been referred to be Nephelometric Turbidity Units (NTU), which measures the angle of the light beam that is scattered back from the particles in the water column (Scheffer 1998). In addition, Secchi disk reading is a common method used for measuring water transparency in lakes. However, in shallow lakes Secchi disc readings can be unreliable due to visibility exceeding water depth, thus chlorophyll *a* can be used as an indicator of water transparency.

Granqvist & Mattila (2004) suggested that clay turbidity of 3 NTU equals to a Secchi-disc depth of approximately 4 meters and 35 NTU to about 0.5 meters. The concentration of suspended material expressed, as mg l⁻¹ is not a reliable estimate of turbidity since the size and shape of the suspended particles influence light behaviour having different effects on the vision of fish.

1.3 Turbidity and fish predation

Most fish species have well-developed eyes and depend on vision as the main source of sensory information (Guthrie & Muntz 1993). Since fish inhabit a wide spectrum of light environments in natural waters, their visual adaptation varies considerably from species to species (Wootton 1990). Some species are adapted to feed at low light levels and are active during twilight and night (pikeperch *Sander lucioperca* (L.)) (Vandenbyllaardt et al. 1991), while some species prefer good light conditions and feed actively during the day (perch *Perca fluviatilis* L., bluegill *Lepomis macrochirus* Rafinesque) (Vinyard & O'Brien 1976, Ali et al. 1977). Some cyprinid species common in European temperate lakes, such as white bream (*Abramis björkna* (L.)), bream (*Abramis brama* (L.)) and roach (*Rutilus rutilus* (L.)), are known to be active in foraging at low light intensities and prefer dusk and dawn for feeding (Zadorozhnaya 1978, Lammens et al. 1987, Diehl 1988, Van Den Berg et al. 1994). Fish species that inhabit clear-water habitats most of their lives show different physiological and morphological properties such as larger eyes, more developed retina and vision-related neural structures compared to species inhabiting turbid environments (Huber & Rylander 1992, Huber et al. 1997). On the other hand, there are fish such as pikeperch and ruffe (*Gymnocephalus cernuus* (L.)) that are equipped with *Tapetum lucidum*, a reflective material in their retina, which gives them an advantage in turbid and low light environments.

Suspended sediments increase light attenuation through water (Kirk 1983)

decreasing the penetration of light and reducing the visual range of animals that mainly use their vision for foraging (Davies-Colley & Smith 2001). Turbidity can reduce visibility in the water column by scattering and absorption of light (Lythgoe 1979). Light behaves differently with organic and inorganic particles in the water. Organic turbidity results in the absorption of light while inorganic matter mainly scatters light (Kirk 1981). The scattering of light has more pronounced effects on the feeding of fish since it interferes with the background light level and reduces contrast between the prey and its background. Contrast between the prey and its background is more important than the absolute light level for fish to be able to detect prey in the water column (Hemmings 1966). The characteristics of the prey such as size, pigmentation, and motion also play an important role in detection of the prey for visually foraging fish (Confer et al. 1978, O'Brien 1987b, O'Keefe et al. 1998).

Piscivorous and planktivorous fish are affected by turbidity in different ways mainly due to the different size of prey they consume (De Robertis et al. 2003). In clear water and under high light intensity, piscivorous fish are able to detect their fish prey from a greater distance than planktivorous fish can detect the smaller-sized planktonic prey (Breck 1993, Utne 1997, Vogel & Beauchamp 1999). An increase in turbidity could be more beneficial for planktivorous fish because their encounter rates with piscivorous predators are reduced more than their encounter rates with their planktonic prey (De Robertis et al. 2003). This is similar to fog, which has little effect on short-range vision but can greatly diminish the visibility of objects at a distance (Lythgoe 1979), which also supports the "turbidity as cover" hypothesis (Gregory 1993, Aksnes & Utne 1997, Gadomski & Parsley 2005). The size-selective predation of planktivorous fish on zooplankton was found to be unaffected in turbid water conditions (Hecht & Van Der Langen 1992). Some planktivorous fish can switch to filter-feeding obtaining an advantage over piscivorous fish in turbid

conditions (Lammens et al. 1987, Van Den Berg et al. 1994).

Certain fish species can use non-visual senses such as chemical (olfaction) (Vilhunen & Hirvonen 2003, Lehtiniemi et al. 2005) and mechanical senses (lateral-line system) (Wootton 1990, Mogdans 2005) for detecting prey. Predator fish that locate their prey by non-visual senses may not be affected by turbidity (Rowe et al. 2003). Juvenile Atlantic cod (*Gadus morhua* L.) were able to locate their prey in highly turbid waters using a combination of both vision and chemoreception (Meager et al. 2005).

The reaction distance is the distance at which the fish first detects its prey and starts the attack (Vinyard & O'Brien 1976, Utne-Palm 2002). Many studies have shown that the reactive distance of the predator changes with environmental conditions such as turbidity, light intensity, prey size and structural complexity (Vinyard & O'Brien 1976, Diehl 1988, Utne-Palm 1999, Vogel & Beauchamp 1999). With increasing turbidity, the reactive distance of the predator will shorten, increasing the probability of the prey detecting the predator before the predator detects them (Abrahams & Kattenfeld 1997).

Utne-Palm (2002) reviewed the physical and behavioural aspects of visual feeding by fish in a turbid environment and suggested that turbidity can have both positive and negative effects on predator fish. The reactive distance of smallmouth bass (*Micropterus dolomieu* Lacepède) decreased nonlinearly with increasing turbidity (Sweka & Hartman 2003). Most turbidity studies have measured the reactive distance to determine the effects of turbidity on the predator and found that the reaction distance of planktivorous fish to its planktonic prey decreased with increasing turbidity (Vinyard & O'Brien 1976, Barrett et al. 1992, Gregory & Northcote 1993, Miner & Stein 1993, Benfield & Minello 1996, Utne 1997, Utne-Palm 1999). Some studies have tested the feeding efficiency of the predator by prey consumption in turbid environments

and found the effects of turbidity on feeding efficiency to be negative (Reid et al. 1999, Macia et al. 2003, De Robertis et al. 2003, Horppila et al. 2004, Nurminen & Horppila 2006).

Increased turbidity can also lead to enhanced feeding motivation caused by a reduced risk of predation. The highest feeding rates of juvenile chinook salmon (*Oncorhynchus tshawytscha* Walbaum) occurred at turbidity levels of 35 to 100 NTU, which was linked to the possible decrease in predation risk (Gregory 1993). Fathead minnows (*Pimephales promelas* Rafinesque) increased their feeding in turbid water compared to clear water in the presence of predators (Abrahams & Kattenfeld 1997). Smelt (*Osmerus eperlanus* L.) consumed the highest number of *Chaoborus flavicans* (Meigen) at 30 NTU in the experiments conducted by Horppila et al. (2004). Fish may have higher feeding rates at intermediate turbidity levels due to the increase in the contrast between the prey and its background (Boehlert & Morgan 1985, Bristow & Summerfield 1994, Utne 1997, Utne-Palm 1999). Several studies also found that increased turbidity had no effect on prey consumption of fish (Breitburg 1988, Flik et al. 1997, Reid et al. 1999, Granqvist & Mattila 2004).

1.4 Turbidity and distribution of fish

The indirect effects of predation commonly result in the movement of prey to more beneficial and safer habitats (Lima 1998). The ideal free distribution theory assumes that organisms select habitats that maximize their rate of food intake (Kennedy & Gray 1993). On the other hand, some studies have shown that predation risk is the main factor for habitat shifts (Lima & Dill 1990), while other studies have suggested that the spatial complexity is the determining factor (Lewin et al. 2004). Structurally complex macrophyte stands found in the littoral act as good refuge for small fish and zooplankton (Persson & Eklöv 1995, Schriver et al. 1995). Macrophytes are important in shallow lakes and often

cover large areas (Scheffer 1998, Nurminen 2003). In shallow lakes horizontal migration is commonly observed for zooplankton and fish since the possibilities for vertical migration are limited due to low water depth. Young fish conduct diel horizontal migrations between the littoral covered with vegetation and the open water (Bohl 1980, Gliwicz & Jachner 1992, Jacobsen & Berg 1998, Okun et al. 2005).

Diel patterns in the distribution of fish are strongly affected by biotic interactions (Helfman 1978) as well as abiotic conditions (Townsend & Risebrow 1982). Predators can move to habitats with available prey and maximize their energy intake at certain times of the day (Hall et al. 1979, Bohl 1980, Wurtsbaugh & Li 1985). Moreover, fish conduct diel habitat shifts in order to avoid competition (Werner & Hall 1979) and to reduce predation risk (Hanych et al. 1983, Diehl & Eklöv 1995). Diel habitat shifts may affect the chances of a predator encountering its prey consequently affecting predator-prey dynamics.

Turbidity plays a significant role in the distribution of fish (Blaber & Blaber 1980, Skov et al. 2002, Jacobsen et al. 2004). Jeppesen et al. (2006) found major changes in the habitat distribution of roach and perch along a trophic state gradient in a study including 34 Danish lakes. Several fish species have shown to actively choose turbid water over clear water during the early stages of life (Blaber & Blaber 1980, Levy & Northcote 1982, Cyrus & Blaber 1987, De Graaf et al. 1999, Emmet et al. 2004). The advantages of turbid water to juvenile fish were linked to reduced predation pressure where turbidity could act as a protective cover (Gregory 1993, Gregory & Levings 1998). Turbidity can also decrease the costly anti-predator behaviour of prey fish (Lehtiniemi et al. 2005) and increase the energy gain for growth. Larval Pacific herring (*Clupea harengus pallasii* Valenciennes) lowered their activity levels in turbid water due to reduced predation risk and showed a better growth rate (Fiksen et al. 2002)

Snickars et al. (2004) showed experimentally that 0+ perch (2.5-5 cm total length) reduced the usage of vegetated habitats at turbidity levels > 25 NTU. Roach (13-25 cm total length) dispersed all over the lake during the day in turbid Lake Sobygård, but aggregated in the littoral during the day in clear Lake Stigsholm (12-23 cm total length), both shallow lakes in Denmark (Jacobsen et al. 2004). Compared to clear water, 0+ pike (*Esox lucius* L.) in turbid water distributed more randomly among habitats showing no preference for complex habitats (Skov et al. 2002). The above studies suggested that turbidity could act as a refuge in natural habitats. The presence of vegetation and turbidity in lakes often change reciprocally; vegetation reduces turbidity while turbidity has a negative effect on vegetation (Scheffer 1998). Macrophytes compete for nutrients with phytoplankton and reduce resuspension of sediment. In clay-turbid lakes, turbidity creates a low light level environment preventing macrophytes from developing.

2. Aims of the thesis

The main aim of the thesis was to clarify the **effect of turbidity on:**

1- The feeding of perch and white bream

Laboratory experiments were conducted (**I, II & III**) with perch (*Perca fluviatilis* L.) and white bream (*Abramis björkna* (L.)), two fish species common in temperate lakes in Europe. The aim was to determine if elevated clay turbidity affected the feeding efficiency of perch and white bream (Fig. 1). Additionally the aim was to clarify the effects of turbidity on predator preying on different types of prey, pikeperch larvae (*Sander lucioperca* (L.)) (**I**), *Daphnia pulex* (Leydig) (**II**), *Sida crystallina* (O.F. Müller) (**II**) and *Chaoborus flavicans* (Meigen) (**III**).

2- The distribution of perch, roach and white bream

The distribution of perch, roach (*Rutilus rutilus* (L.)) and white bream with changing turbidity and macrophyte presence was investigated within a lake (**IV & V**) and between two lakes (**VI**) (Fig. 1). The main aim was to clarify the effects of clay turbidity on the diel horizontal migration of perch, roach and white bream (**IV & V**). The goal was also to determine the effects of phytoplankton-induced turbidity on the distribution of roach and perch in a 15-year study in two shallow lakes subjected to changes in trophic state (**VI**).

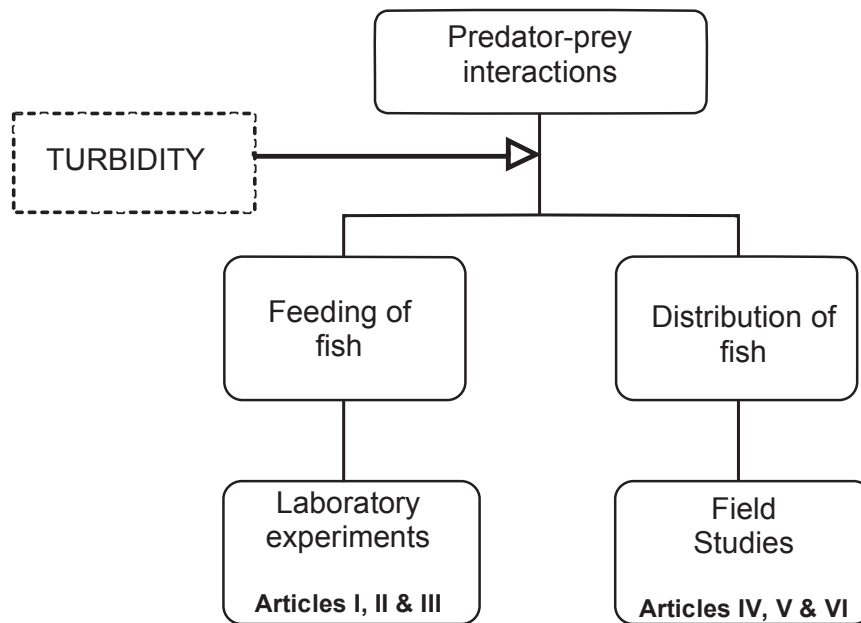


Figure 1. Schematic summary of the organization of the study.

3. Materials and Methods

3.1 Laboratory experiments

Experiments (I, II & III) were conducted in transparent plastic bags, which were placed in aquaria filled with water (Fig. 2). The aquaria were covered with black plastic in order to avoid visual disturbance from outside. The perch - *Sida* (II) experiments were conducted



Figure 2. The experimental set-up used in articles I, II & III.

in non-transparent plastic boxes and *Nuphar lutea* (L.) leaves were placed in each box. Turbidity levels were created before the fish were added to the bags and boxes with clayish bottom sediment and slight air bubbling was used to prevent sedimentation of the suspended material. After each experiment fish were taken out and water temperature, pH, turbidity and concentration of dissolved oxygen were measured with a YSI-6600 sonde. At the end of each experiment, light intensity (wavelength 400-700 nm) in the air and in the bags and boxes was measured with a LI-1400 datalogger equipped with quantum sensors. In the experiments there were 3 fish in each bag and box. The duration of each set of experiments was determined by preliminary experiments. Thus, the experiments lasted 2 hours in articles I & III and half an hour and 2 hours in article II. After each experiment, fish were captured from the bags and experimental units, weighed to the nearest gram, measured to the nearest mm (total length) and analysed for the number of swallowed prey.

Perch, caught from Lake Kivijärvi located in southern Finland were acclimatized for 2-3 weeks in the laboratory and pikeperch larvae were obtained from cultures (I). In article II,

Table I. Summary of the experimental set-up in articles I, II & III.

ARTICLE	Predator Total length (cm)	Prey Length (mm)	Number of Prey (ind)	Water temp (°C)	Volume of water (l)	Turbidity range (NTU)	Main statistical methods
I	Perch (<i>Perca fluviatilis</i>) (6-11)	Fish larvae <i>Sander</i> <i>luciperca</i> (4.4-6.5)	100 & 200	16	10, 15, 20, 25, 35 & 45	5-85	Logistic Regression
II	Perch (<i>Perca fluviatilis</i>) (6-8) & (7-9)	Zooplankton <i>Daphnia pulex</i> (1-1.5) & <i>Sida</i> <i>crystallina</i> (1-1.5)	200 & 75	18 & 18	15 & 10	0-50 & 0-30	ANOVA
III	White bream (<i>Abramis</i> <i>björkna</i>) (9-14)	Invertebrate predator <i>Chaoborus</i> <i>flavicans</i> (9-11)	100	15	42	10-50	ANCOVA

perch were captured with a seine net from a eutrophic and clay-turbid Lake Tuusulanjärvi located in southern Finland and acclimatized in the aquarium for 2 weeks. *Daphnia pulex* were cultured in the laboratory and fed on the green algae (*Chlorella*) (II). *Sida crystallina* and collected leaves (*Nuphar lutea*) were cultured in a big bucket equipped with air bubbling. White bream were caught with seine nets from Lake Tuusulanjärvi and acclimatized for 3 weeks in the laboratory. The fourth instar larvae of *Chaoborus flavicans* were caught with net hauls and bottom sampling from clay-turbid Lake Hiidenvesi. A summary of the experimental set-up in articles I, II & III is given in Table 1.

3.2 Field studies

Study areas

The diel horizontal migration studies IV & V were carried out at the Kirkkojärvi basin (1.6 km²) in the north-western part of Lake

Hiidenvesi (60° 24' N; 24° 18' E), a large (30.3 km²) eutrophic lake in south-west Finland. The Kirkkojärvi basin is shallow (mean depth 1.1 m, maximum depth 3.5 m) and clay-turbid (40 NTU, Secchi depth ≤ 0.5 m) with few submerged macrophytes (*Myriophyllum verticillatum* L., *Potamogeton obtusifolius* Mert. & Koch) and wide zones of floating-leaved plants (*Nuphar lutea* (L.), *Nymphaea alba* L.) (Nurminen 2003). The basin also includes beds of emergent macrophytes (*Typha angustifolia* L., *T. latifolia* L., *Glyceria maxima* (Hartm. Holmb.). The fish assemblage is dominated by cyprinids, for example roach, white bream, and bleak (*Alburnus alburnus* L.) (Vinni et al. 2000, Olin & Ruuhijärvi 2005). A summary of the fish sampling in the field studies conducted in articles IV, V & VI are given in Table 2.

In article VI, fish samples were collected from 1988 to 2002 in shallow and eutrophic Lake Væng and Lake Søbygård situated in central Jutland (56° N; 9° E), Denmark. Lake

Table 2. Summary of fish sampling in the field studies conducted in articles **IV**, **V** & **VI**. Fish were divided into size classes according to the length frequency distributions and their diet.

ARTICLE	Study site	Date	Sampling method	Sampling area & Turbidity	Timing of sampling	Duration of sampling & Number of nets	Studied fish species & Size classes	Main statistical method
IV	Kirkkojärvi basin	August 2002	NORDIC-multimesh gillnets	littoral & open water 10-30 NTU	Full day light to total darkness (every 2 hours)	30 minutes 3 nets	Roach Perch white bream (≤ 11 , > 11 cm)	Repeated-measures ANOVA
V	Kirkkojärvi basin	August 2003	NORDIC-multimesh gillnets	Submerged macrophytes 4 NTU, floating-leaved macrophytes 19 NTU & open water 38 NTU	dawn, dusk and night	1 hour 4 nets	small & large perch (≤ 8 , > 8 cm)	Repeated-measures ANOVA
VI	L.Væng & L.Søbygård	15 Aug - 15 Sept 1988 to 2002	NORDIC-multimesh gillnets & Electrofishing	littoral & lake centre in each section L. Væng 5 sections 1.5 and 0.9 m Secchi depth L. Søbygård 6 sections 0.6 m Secchi depth	Dusk to dawn	18 hour 3 nets in each section	Roach (≤ 8 , > 8 cm) Perch (≤ 10 , > 10 cm)	Restricted maximum likelihood in a linear mixed model

Væng (16 ha) has a mean depth of 1.2 m and Lake Søbygård (40 ha) of 1 m. Lake Væng was divided into five and Lake Søbygård into six sections consisting of equal sized pies with a mid-lake station acting as centre. Between 1989 and 1996 Lake Væng was clear (chlorophyll *a* 21 µg l⁻¹) and macrophytes were present. In 1988 and from 1997 to 2002 the lake was turbid (chlorophyll *a* 53 µg l⁻¹) and macrophytes disappeared. Lake Søbygård was turbid (chlorophyll *a* 125-197 µg l⁻¹) during the entire study period from 1988 to 2002. For Lake Væng, the data series were divided into two periods covering years with and without submerged macrophytes, respectively (VI). Macrophytes were present from 1989 to 1996, absent in 1988 and from 1997 to 2002. For comparative purposes, the same time period was used for Lake Søbygård even though submerged plants were absent during the entire study period (VI).

In articles IV & V, the potential predators in Lake Hiidenvesi were pike, pikeperch (> 6 cm) in the open water and perch (> 8 cm). In article VI, pike > 20 cm and pikeperch > 6 cm were potential predators for roach and perch.

4. Results and discussion

4.1 Feeding of perch and white bream

In the laboratory experiments conducted with perch feeding on pikeperch larvae, the probability of pikeperch larvae being eaten decreased with increasing clay turbidity (I) (Fig. 3). This result supports previous studies where turbidity reduced predation pressure on young fish by providing a protective cover, thus reducing the risk of being detected and eaten (Gregory 1993, Gregory & Northcote 1993). Since container size is known to influence predation in experimental studies (Kaiser 1983, De Lafontaine & Leggett 1987), the data were divided into two groups based on water volume (10-20 and 25-45 l) (I). Turbidity had a significant effect on the probability of pikeperch larvae being eaten in both volume groups, whereas the density of larvae was only significant in larger volumes (25-45 l) (I). A lower encounter rate between predator and the prey will lower the probability of predation

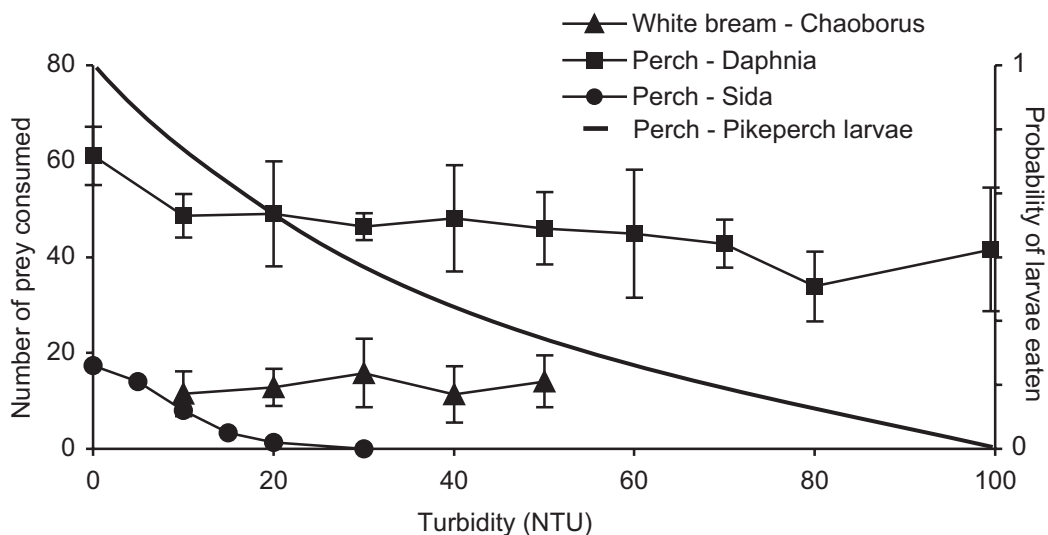


Figure 3. Effects of turbidity on the feeding of perch on pikeperch larvae, *Daphnia pulex* and *Sida crystallina* and white bream feeding on *Chaoborus*. The feeding efficiency of perch (II) and white bream (III) are given on the y-axis. Note the different density of prey used in the experiments. Each point corresponds to the average number of prey consumed at each turbidity level. The lines represent 95% confidence limits. The secondary y-axis shows the probability of pikeperch larvae eaten (I).

(Eggleston 1990, Wong & Barbeau 2003). The density of prey is important in the foraging behaviour and consumption of predator fish (Walton 1980). In article **I**, probably the decrease in the density of prey reduced the chances of encounter and being eaten by the predator. The results (**I**) coincide with Utne (1997) and Sandström (2004) who found that the reaction distance declined faster in low than in high prey densities with increasing turbidity. Turbidity may affect prey capture more severely at low prey densities (Breitburg 1988). This could be due to low encounter rate combined with increased search time due to the reduced visual range of the predator.

In the experiments with perch and free-swimming *Daphnia pulex*, the highest feeding rate by perch was observed at 0 NTU whereas feeding showed a 20% decrease at 10 NTU, remaining at almost the same rate up to 50 NTU (**II**) (Fig. 3). The same experiments were conducted up to 100 NTU and the feeding efficiency did not change significantly (Nurminen unpublished) (Fig. 3). The findings coincide with Granqvist & Mattila (2004) where turbidity levels up to 30 NTU and twilight conditions did not

reduce the ability of young perch to capture mysids. Several other studies also showed that increasing turbidity had no effect on predation by perch and other fish species (Breitburg 1988, Flik et al. 1997, Reid et al. 1999).

The type of prey differed in experiments **I** and **II**. Size, colour and swimming differ between the types of prey and are important for detection by vision-oriented fish (O'Keefe et al. 1998, Utne-Palm 2002). The background contrast changes with the colour and size of the prey (Hemmings 1966, Hinshaw 1985, Giske et al. 1994). Increasing turbidity levels affected the reactive distance of bluegill to large prey much more than to small prey up to a certain level of turbidity, but at high turbidity and low light levels the reactive distance was independent of prey size (Vinyard & O'Brien 1976). A relatively higher predation risk was predicted for smaller zooplankton compared to large zooplankton with increasing turbidity in the studies of Miner & Stein (1993) and Giske et al. (1994). Large zooplankton are more vulnerable to predation in clear water compared to small zooplankton

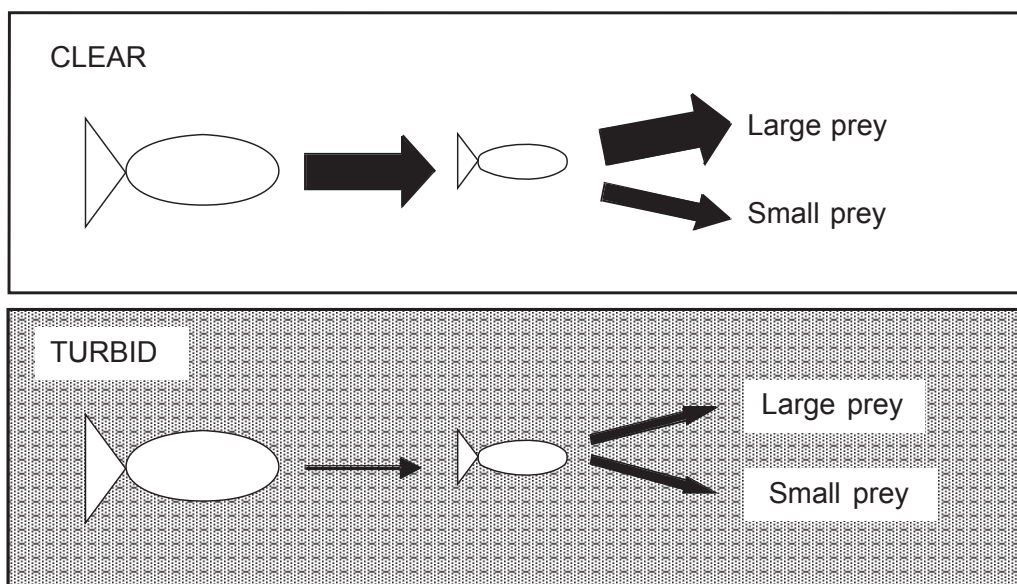


Figure 4. The suggested effects of turbidity on fish predation. The predation pressure of piscivorous fish (large fish) on planktivorous (small fish) fish in a clear and turbid environment. The planktivorous fish are predating on small and large prey. The thickness of the arrows shows the strength of predation exerted on the following trophic level.

and planktivorous fish are known to feed size selectively on large zooplankton. The reaction distance of the predator to large prey is longer compared to small prey in clear water. However, when turbidity increases the reaction distance of the predator to large prey shortens more compared to the reaction distance to small prey and the search volume for the planktivore may become the same for both sizes of prey after a certain level of turbidity. In experiments I & II, perch continued feeding on *Daphnia* (1-1.5 mm) while increasing turbidity reduced the feeding of perch on pikeperch larvae (4-6 mm). This result coincides with the previous study where large prey were more affected by increasing turbidity compared to planktonic prey (De Robertis et al. 2003) (Fig. 4).

There was a significant decrease in the feeding rate of perch on plant-attached prey *Sida crystallina* with increasing turbidity (0-30 NTU) (II) (Fig. 3). In the case of plant-attached prey, the predator probably does not benefit from the increasing contrast between the prey and its background provided by increasing turbidity since there is no water between the prey and the leaf. Additionally the light attenuation, an important factor for detection of prey, increases steeply under floating-leaved plants (Nurminen & Horppila 2006). The substantial decrease in the feeding efficiency of perch on *Sida* with increasing turbidity was suggested to be due to the strong effect of turbidity on motionless attached prey. Moreover, the light environment underneath the leaves is unfavourable for prey detection because of the effects of the leaves on the spectral composition, direction and intensity of light. *S. crystallina* is known to perform pronounced diel migrations as a trade off behaviour for avoiding predators and reaching food resources. They stay attached to the floating leaves during the day and switch to free-swimming mode at night (Fairchild 1981, Nurminen et al. 2005). This migratory behaviour is also probably triggered by changes in the light climate under the leaf and in the open water (Nurminen et al. 2007). Turbidity probably provides a safer

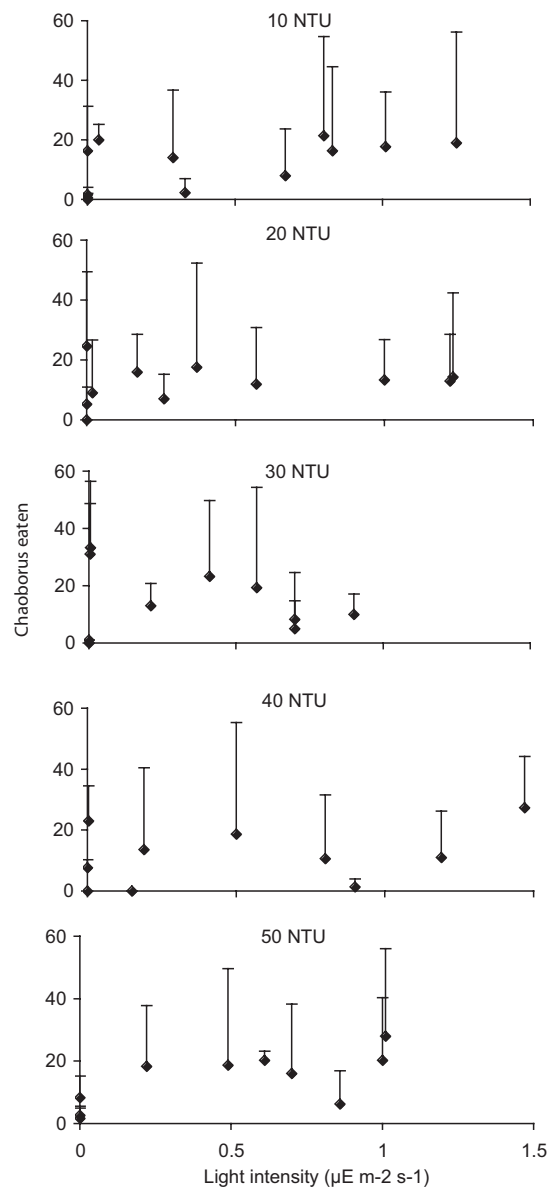


Figure 5. The combined effects of turbidity and light intensity on the average number of *Chaoborus* consumed by white bream. Each dot corresponds to one bag with three fish. The lines represent 95% (+) confidence limits (III).

environment for *S. crystallina* attached to the floating leaved macrophytes (II).

The combined effect of light and turbidity did not have a significant effect on white bream feeding on *Chaoborus flavicans* (III) (Fig. 5). Both light and turbidity can limit the foraging of fish (Confer et al. 1978, Miner & Stein 1993, Greacy & Targett 1996). To clarify

the interactive effects of light and turbidity on the feeding of white bream, 8-10 different light levels were used for each turbidity level (III). Feeding rates increased at very low light levels and remained high at most light and turbidity levels (Fig. 3, Fig. 5). The effects of light and turbidity level can have an interactive effect on fish predation (Miner & Stein 1993). Gulf killifish (*Fundulus grandis* Baird & Girard) feeding was not affected by low light intensity but when light intensity was kept constant and the turbidity level was increased, their predation rate decreased (Benfield & Minello 1996) indicating the importance of light scattering. In article III, light had a significant effect on the feeding of white bream while turbidity did not. However, when the dark experiments were left out of the analysis, there was no significant effect of light or turbidity.

Utne-Palm (2002) suggested that at medium to high light levels turbidity could have a positive effect on visually feeding fish by improving the contrast between the prey and the background. However, at low light levels the detection of prey may be limited by absolute light instead of only the scattering of light (Miner & Stein 1993). On the contrary, the findings of experiment III showed that the feeding rate of white bream was high at low light levels ($0-0.5 \mu\text{E m}^{-2} \text{s}^{-1}$). Predation rate by cyprinid adult creek chub (*Semotilus atromaculatus* (Mitchill)) on cyprinid prey juvenile black nose dace (*Rhinichthys atratulus* (Hermann)) was higher at twilight compared to high light conditions (Cerri 1983). This was suggested due to the higher activity of this cyprinid predator at twilight. White bream are known to feed actively at dusk (Zadorozhnaya 1978, IV). The experiments (III) suggest that white bream feeding is not hampered by low light levels.

In the dark, the feeding of white bream was low and no prey was consumed in most of the experiments (III). This suggests that white bream depend mainly on vision for feeding. Cyprinids are known to filter-feed however they are less efficient at filter-feeding large

zooplankton prey ($> 1 \text{ mm}$) (Van Den Berg et al. 1994). *C. flavicans* are *c.* 10 mm in size and are rapid swimmers (Pastorok 1980), thus, white bream probably were not able to use filter-feeding in the experiments (III).

Prey behaviour

Prey have different capabilities for escaping from a predators (Wanzenböck 1992). Some prey swim faster as observed by O'Keefe et al. (1998), the swimming speed of *Daphnia* differed between different clones. *Daphnia* can also exhibit different behaviour patterns such as 'hop-and-sink' and 'zooming' (Dodson et al. 1997). Pikeperch larvae show a spiral upward swimming in the water column during the few days after hatching (Schlumberger & Proteau 1996). The difference in prey movement can affect the feeding efficiency of predator fish and probably this had an effect in our experiments with perch as the predator (I & II).

Chaoborus are sensitive to light intensities and have an upper tolerance limit of $1.8 \mu\text{E m}^{-2} \text{s}^{-1}$ (Teraguchi & Northcote 1966, Wagner-Döbler 1988). In nature, they avoid high light levels by conducting vertical migration and stay in the deep layers during the day (Liljendahl-Nurminen et al. 2003). In the experiments (III), chaoborids were eaten in high numbers when the water volume with tolerable light ($< 1.8 \mu\text{E m}^{-2} \text{s}^{-1}$) decreased. This indicated that *C. flavicans* moved down in the bags to avoid the light, increasing their density at the bottom of the bag and also their chances of being eaten by white bream. Furthermore, Horppila et al. (2004) showed that at high light levels smelt fed on *C. flavicans* in high numbers. At tolerable light levels they can distribute around the bag, which should lower the risk of predation by white bream due to increased foraging volume (III). However, in the experiments (III), the highest feeding efficiency of white bream was observed at lowest light levels. This again suggests that white bream are efficient feeders at low light levels.

Limitations in laboratory experiments

The main purpose of laboratory experiments is to control environmental conditions and try to elucidate a single or only a few processes. Some authors have argued that microcosm experiments have serious limitations (Carpenter 1996). In predation experiments, the mortality rate of prey could be affected by the size of the container (Bergström & Englund 2002). Experimental duration is known to affect results (Bloesch et al. 1988, Redi et al. 1999). However, Drenner and Mazumder (1999) have argued that microcosm and whole lake experiments have showed similar community responses as in natural conditions to regulations such as nutrient and planktivorous fish. They agreed that results must be applied with caution to larger scale systems but they could give very useful information for the complete understanding of how lakes systems function (Drenner & Mazumder 1999).

There was large variation between individual fish in the bags in the experiments (**I**, **II** & **III**). There was always one fish that did not consume any prey while one fish consumed high numbers of prey. This variation is probably due to the behaviour known in ecology as aggression syndrome, where some individuals are more aggressive than others across a range of situations (Sih et al. 2004). This variation may occur between individuals of the same population that compete for resources (Ward et al. 2004). Individuals can be classified as shy or bold and may react differently when faced with predation, inter or intra species interactions, reproduction, habitat exploration and dispersal (Wilson et al. 1994).

The experimental set-ups are spatially limited. In nature, prey could move to a safer habitat and escape from the predator. However, in an experimental set-up due to the restricted space, the chance of being caught by a predator is high. In addition, the limited space means the effect of turbidity on long reaction distance may not be detected. Therefore, the

effects of turbidity could be underestimated in small experimental units. Luckingbill (1974) showed that large container sizes reduced predation rates by lowering the encounter rate between the predator and prey. On the other hand, long narrow aquariums increased the reaction distance of yellow perch (*Perca flavescens* Mitchill) (Confer et al. 1978). Comparisons of predation over a large range of container sizes could be problematic as observed in the experiments in article **I**.

4.2 Distribution of perch, roach and white bream

4.2.1 Role of turbidity in diel horizontal migrations

Perch and roach (≤ 11 cm) showed diel horizontal migration between the littoral and the pelagic zone in Kirkkojärvi basin (**IV**). The average catch of perch and roach (≤ 11 cm) was highest at the pelagic zone at dusk (21:00) (Fig. 6). Previous studies have shown that juvenile fish migrate from the macrophyte beds where they spend the day, out to the open water at night (Bohl 1980, Gliwicz & Jachner 1992, Jacobsen & Berg 1998). The average number of perch > 11 cm increased in the littoral and decreased in the pelagic at dusk (**IV**) (Fig. 6). The high proportion of *Leptodora kindtii* (Focke) and *Limnosida frontosa* Sars in the stomach of perch ≤ 11 cm in the pelagic zone indicate that probably perch ≤ 11 cm benefit from large zooplankton in the pelagic zone at dusk. The reasons behind the migrations of perch and roach (≤ 11 cm) to the pelagic zone at dusk were probably to avoid predation by large perch and the benefit gained from the large-sized zooplankton in the pelagic zone. A turbidity level of c. 40-60 NTU also created a safe environment for perch and roach (≤ 11 cm) allowing them to migrate to the pelagic (**IV**).

The stomach contents of perch ≤ 11 cm caught in the pelagic at dusk included *Sida crystallina* indicating their migration from the littoral

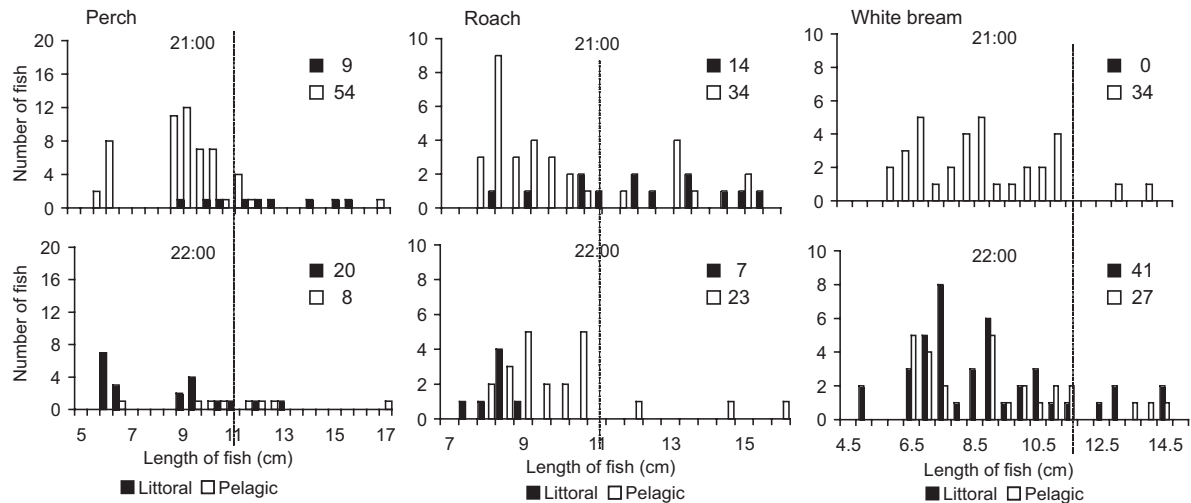


Figure 6. Length frequency distribution of perch, roach and white bream at 21:00 (dusk) and 22:00 (night), in littoral and pelagic zones in Kirkkojärvi basin. The dotted vertical lines show the division of the size classes for fish ≤ 11 cm and > 11 cm. The total number of fish caught in the littoral and pelagic zone are given. Modified from article **IV**.

(**IV**). *S. crystallina* is a plant-associated filter feeder inhabiting the littoral zone and it does not occur in the pelagic zone (Nurminen et al. 2005). Perch ≤ 11 cm must have fed on them in the littoral and then migrated to the pelagic zone at dusk (**IV**). The diet of roach caught from the pelagic zone at dusk included plant material consisting of macrophytes and epiphytes, found only in the littoral (**IV**).

Perch showed diel horizontal migration also in the other study conducted in Kirkkojärvi basin (**V**) (Fig. 7). Perch ≤ 8 cm were caught in high numbers in the day time in the open water and migrated to the zone covered with floating-leaved macrophytes at dusk. Correspondingly, the highest daytime catch of perch > 8 cm was also observed in the open water (Fig. 7). However, in our study the proportion of fish in the stomachs of perch > 8 cm was very low, indicating low success in piscivorous feeding in the turbid open water. Turbidity (38 NTU) can be acting as a protective cover for perch ≤ 8 cm in the open water (**V**). One of the important factors in habitat choice for a prey fish is the low predation risk (Werner et al. 1983). Environmental conditions such as habitat complexity and turbidity can play an

important role as refuge for prey (Crowder & Cooper 1982, Miner & Stein 1996). The stomach contents of perch ≤ 8 cm in the open water at dusk showed a high proportion of *Limnospira frontosa* indicating that turbidity did not prevent perch ≤ 8 cm from preying on large-sized zooplankton.

A commonly observed pattern for diel horizontal migrations in non-turbid lakes is that small fish inhabit the littoral area with structural complexity during the day and then move to the adjacent open water at night (Bohl 1980, Jacobsen & Berg 1998, Okun & Mehner 2005). The reasons behind this behaviour have been explained as a trade-off between reduced predation risk and optimal foraging for food (Hanych et al. 1983, Gliwicz & Jachner 1992, Diehl & Eklöv 1995). However, based on our diel horizontal migration studies (**IV** & **V**), the timing of migration can change with elevated turbidity levels. Since migration is triggered by changes in light (Reebs 2002), increasing turbidity may change the light level in the water column affecting the behaviour of fish.

In article **IV** perch ≤ 11 cm inhabit the turbid

(40-60 NTU) open water at dusk while in article V perch ≤ 8 cm moved from the turbid (38 NTU) open water to the floating-leaved macrophyte zone with intermediate turbidity (19 NTU) at dusk. In article IV perch ≤ 11 cm were avoiding the floating-leaved zone where perch > 11 cm were present. Perch are known to be successful in feeding in complex habitats and the turbidity in the floating-leaved macrophytes was only about 10-30 NTU (IV). In article V perch ≤ 8 cm were avoiding the turbid open water where pikeperch, which are adapted to see in turbid conditions, were present. It seems in both articles (IV & V) perch (≤ 11 cm and ≤ 8 cm) seem to be avoiding the habitat where predators are present.

Zooplankton inhabiting the open water in high numbers only at night indicated that turbidity alone during the day is not a good refuge for small prey such as zooplankton (V) (Fig. 7). This could also be because moderate turbidity levels can provide a good visual contrast between the prey and its background enhancing the feeding of fish on

planktonic prey (Gregory & Northcote 1993, Horppila et al. 2004). Studying the availability of food resources in the lake could give useful information on the habitat choice of fish.

The stomach contents of perch ≤ 8 cm suggested that they continued feeding on zooplankton in the open water during the day (V). Perch ≤ 8 cm positively selected *L. kindtii* and *L. frontosa* during the day in the open water zone and *L. kindtii* at dusk in the floating-leaved zone. Turbidity probably did not have a negative effect on perch ≤ 8 cm feeding on zooplankton in the open water in the day, while perch > 8 cm were not able to feed on perch ≤ 8 cm (V). Fish tend to utilize optimal feeding strategies that maximise their net energy intake. A turbid habitat can play an important role in reducing costly anti-predator behaviour of prey fish and minimise cost in avoiding predators (Gregory 1993, Abrahams & Kattenfeld 1997, Lehtiniemi et al. 2005). Several studies have shown that, turbidity can impede the vision of perch (I, Bergman 1988, Sandström 2004). Experiments in article II suggested that

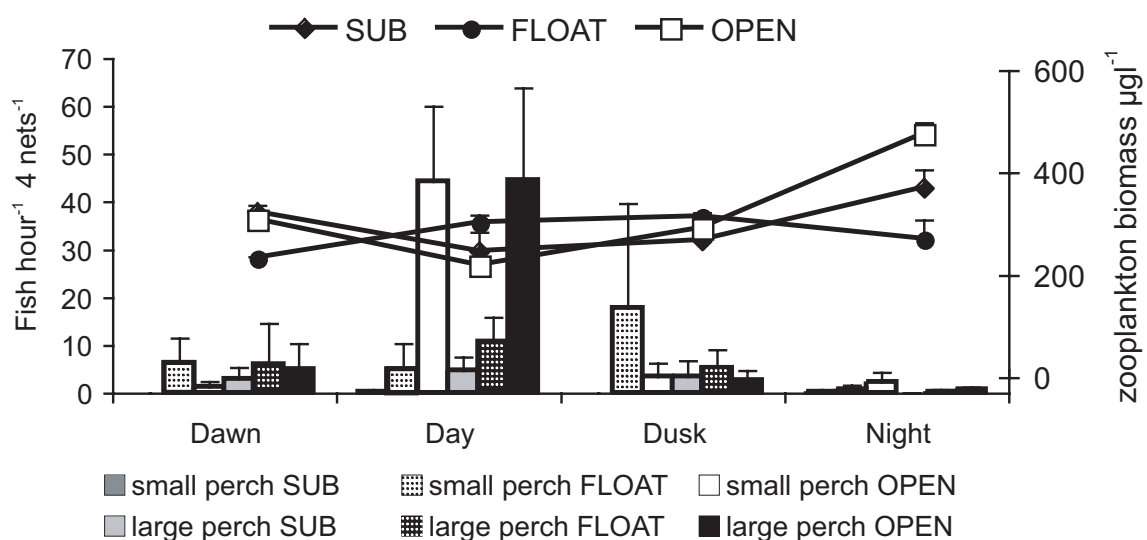


Figure 7. The mean catch (fish hour⁻¹ 4 nets⁻¹) of small perch (≤ 8 cm) and large perch (> 8 cm) at dawn, day, dusk and night in the different zones (submerged macrophyte zone = SUB, floating-leaved macrophyte zone = FLOAT and open water = OPEN) in Kirkkojärvi basin. The biomass ($\mu\text{g l}^{-1}$) of zooplankton including the cladocerans and copepods at dawn, day, dusk and night in the different zones (SUB, FLOAT and OPEN) is given on the secondary y-axis. % 95 confidence limits are shown in vertical lines. Modified from article V.

perch (6-8 cm) feeding on *Daphnia* were not severely affected by turbidity levels up to 100 NTU. Piscivorous fish are known to be more affected by increasing turbidity levels compared to planktivorous fish (De Robertis et al. 2003), because increasing water turbidity reduces the visibility of large prey more than the visibility of small prey (Utne-Palm 2002). The turbid open water could be a safe habitat for perch ≤ 8 cm from perch > 8 cm and perch ≤ 8 cm could still continue feeding on zooplankton (V) (Fig. 4).

White bream (≤ 11 cm) were caught in the pelagic at dusk and increased also in the littoral at night (22:00) (IV) (Fig. 6). The data for article V included the highest catches for white bream (> 8 cm) at dusk and dawn in the open water and the floating-leaved macrophyte zone (Pekcan-Hekim unpublished) (Fig. 8). White bream are known to feed efficiently at low light intensities and to be active at dusk (Zadorozhnaya 1978, Lammens et al. 1987). However, their high feeding efficiency is due to their ability to switch to filter-feeding in low light or dark conditions (Lammens 1985, Diehl 1988, Van Den Berg et al. 1994). Diehl (1988) also showed that roach and bream feeding were favoured in low light levels

compared to perch. The main reason was their ability to switch to filter-feeding but also due to the physiological difference of bream possessing a reflecting material (guanine) in their retina that is lacking in perch. In the experiments (III), the feeding efficiency of white bream (9-14 cm) was not impeded at turbidity levels from 10 to 50 NTU. They were not able to use filter-feeding due to the large size and fast swimming prey and continued particulate feeding. Laboratory experiments (III) and field data (IV & Fig. 8) support that white bream feeding is not affected by low light conditions and turbidity levels up to 50 NTU.

4.2.2 Role of turbidity in distribution of fish in a clear and turbid lake

There was a clear difference for both roach and perch distribution between the period with macrophytes and no macrophytes, in Lake Væng (VI). Roach and perch showed a preference for certain sections in the southern part of the lake in years when there were macrophytes but distributed evenly among the sections when macrophytes disappeared and the lake became turbid (Fig.

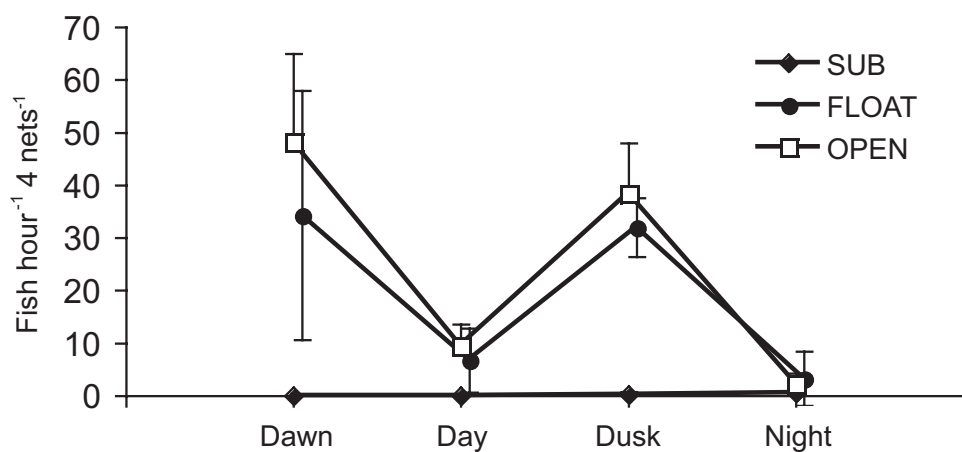


Figure 8. The mean catch (fish hour⁻¹ 4 nets⁻¹) of white bream (> 8 cm) at dawn, day, dusk and night in the different zones (submerge macrophyte zone = SUB, floating-leaved macrophyte zone = FLOAT and open water = OPEN) in Kirkkojärvi basin, Lake Hiidenvesi in 2003. % 95 confidence limits are shown in vertical lines.

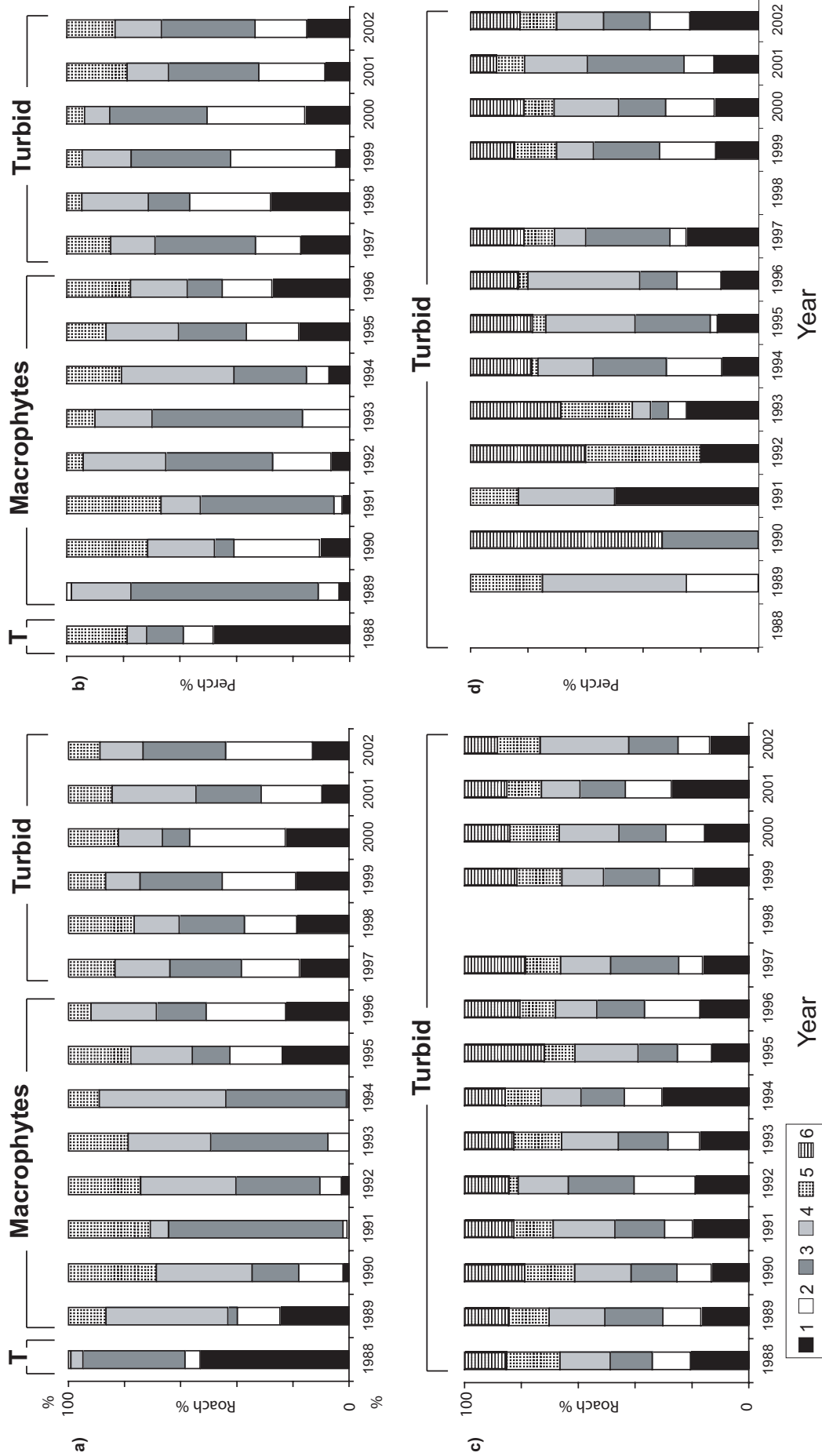


Figure 9. Distribution of all roach and all perch among the five sections numbered 1 to 5 in Lake Væng (a, b), and among the six sections numbered 1 to 6 in Lake Søbygård (c, d), from 1988 to 2002 (**VI**). T and Turbid correspond to the turbid period with no macrophytes and macrophytes present in Lake Væng.

9). In turbid Lake Søbygård, roach and perch both occurred in all sections in almost equal proportions and the pattern did not change during the entire study period (Fig. 9). The distribution of fish is influenced by biotic factors such as predation and competition and also abiotic factors such as turbidity (Donald et al. 2000). Food availability (zooplankton and macroinvertebrate biomass) and water quality parameters such as pH, temperature, and dissolved oxygen were not significantly different between the two periods for both lakes (VI). This suggested that these factors were probably not the determining factors for the distribution of roach and perch in article VI.

After 1994 when plants were more evenly distributed in Lake Væng (1995) or were absent with high turbidity (1996 and onwards), roach and perch increased in the northern part of the lake and occurred in all sections in almost equal proportions (VI). The shift from uneven to even distribution of roach and perch among the sections in Lake Væng corresponds to the decrease in Secchi depth and the increase in chlorophyll *a* concentrations (VI) (Fig. 9). When comparing the size classes, a similar distribution pattern was found for both size classes of perch (perch ≤ 10 and > 10 cm) between the two periods in Lake Væng (VI). However, contrary to roach > 8 cm, roach ≤ 8 cm differed in distribution between the two periods in Lake Væng. They were relatively less abundant in the shallow northern part during the macrophyte years perhaps because of a higher risk of predation by perch in this clear-water state (VI). Increased water turbidity can act as a protective cover allowing fish to disperse evenly among the sections (Skov et al. 2002). Additionally, turbidity could act as a cover for fish from birds (Scheffer 1998). In Lake Søbygård, the Secchi depth remained low with high chlorophyll *a* during the whole study period due to sustained high internal P loading and both size classes of roach and perch were evenly distributed around the lake during the entire study period (VI). Correspondingly, Jacobsen et al. (2004) found that roach (13-25 cm) were foraging in the

pelagic during the day in Lake Søbygård.

In Lake Væng, pike (> 20 cm) occurred in high numbers in 1991 and 1992 and in both years roach ≤ 8 cm and perch ≤ 10 cm avoided the sections where pike was present (VI). However, in turbid Lake Søbygård, with a low abundance of pike, both size classes of roach and perch were found in every section of the lake in almost equal proportions. This suggests that predators may play a role in the habitat choice of roach and perch, but turbidity can contribute to provide a safe environment from predators. The turbidity was caused by phytoplankton in both lakes and shows that it may also act as a good refuge for fish (VI).

4.2.3 Role of macrophytes in distribution of fish

In the zone with submerged macrophytes, perch catches were very low at all sampling times (V). The catchability of gillnets can be low in dense submerged vegetation however, in the same study other fish species such as rudd (*Scardinius erythrophthalmus* (L.)) were caught in high numbers using gillnets (V). Submerged macrophytes are known to provide good refuge for prey fish and zooplankton (Schriver et al. 1995, Jeppesen et al. 1998, Meerhoff et al. 2003). Perch are known to be successful at foraging in structurally complex habitats (Diehl 1988, Persson & Eklöv 1995). However, in Kirkkojärvi basin the zone with submerged macrophytes was not inhabited by perch ≤ 8 cm probably due to the low turbidity (4 NTU) and the presence of pike (V). The results indicate that the water quality effects of submerged macrophytes may negate their structural refuge effect (V). Vegetation provides structural complexity as a refuge by reducing the foraging efficiency of predator fish (Crowder & Cooper 1982). However, it is costly for the prey fish to avoid predators in structurally complex habitats compared to structurally more simple habitats. In a turbid environment, prey can lower its cost on anti-

predator behaviour (Abrahams & Kattenfeld 1997, Lehtiniemi et al. 2005). In the presence of predators, turbidity is probably more beneficial than macrophytes as a refuge for young fish in terms of energy cost. Studies have observed that fish use complex habitats as refuge less when the water is turbid (Snickars et al. 2004). This raises the question: can turbidity alone be a refuge for prey fish from predators when macrophytes are not present? In our study (V), even though perch ≤ 8 cm have a lower supply of food in the open water at daytime when the highest biomass of zooplankton is in the floating-leaved and submerged macrophytes, they might be benefiting from the low cost of anti-predator behaviour and are able to avoid predators.

At dusk, perch migrated to the zone with floating-leaved macrophytes probably because low light combined with high turbidity in the open water impeded the foraging of perch (V). The average catch of pikeperch increased in the open water at dusk which could be threat to small perch since it is known to be successful at feeding in turbid and low light conditions (Vandenbyllaardt et al. 1991). Floating-leaved macrophytes probably provided a good environment for perch at dusk with moderate complexity and turbidity. *L. frontosa* and copepods found from the stomach contents of perch indicate that perch continued feeding in the floating-leaved macrophyte zone (V). Floating-leaved macrophytes are able to colonize in large areas in clay-turbid lakes, while submerged species are limited by light availability and loose bottom substrates (Chambers & Kalff 1985, Nurminen et al. 2005). Floating-leaved species have a weaker effect on sediment resuspension compared to submerged macrophyte forms, providing vegetation and turbidity in the same habitat (Horppila & Nurminen 2005). Floating-leaved macrophytes are also beneficial as refuge area because they are not too complex (Nurminen et al. 2005) and they could decrease the predation threat from above (e.g. birds) (Jacobsen et al. 2004). Intermediate vegetation density was preferred by perch in several studies (Eklöv 1997, Snickars et al.

2004).

The distribution of both size classes of roach and perch showed a statistically significant negative relationship with macrophyte coverage and plant volume infested (VI). Perch prefer complex habitats and have been shown to feed successfully among submerged macrophytes while roach prefer simpler habitats (Diehl 1988, Persson & Greenberg 1990, Persson & Eklöv 1995). During the macrophyte years in Lake Væng, both roach and perch were found in the sections in the southern part of the lake with low macrophyte coverage and plant volume infested (VI). Avoidance of dense macrophyte beds by perch and roach is in accordance with Crowder & Cooper (1982), Werner et al. (1983) and Christensen & Persson (1993), reflecting that high vegetation density impairs the ability of fish to move, thus reducing their foraging efficiency and ability to escape predators (Bartholomew et al. 2000).

5. Conclusions

The laboratory experiments with perch as predator showed that pikeperch larvae benefited more from increasing clay turbidity as a refuge than *Daphnia* (I & II). Increasing clay turbidity levels significantly reduced predation pressure by perch on plant-attached prey *Sida* (II). Increasing clay turbidity levels did not affect the feeding efficiency of white bream on *Chaoborus* (III). However, white bream were not able to feed in total darkness (III).

The main findings of the thesis show that clay turbidity (IV & V) and also phytoplankton-induced turbidity (VI) can play a significant role in the distribution of fish. Perch ≤ 8 cm can use clay turbidity as refuge when macrophytes are present in the lake (V). Floating-leaved macrophytes are probably good refuges for perch ≤ 8 cm in clay-turbid lakes and provide a certain level of turbidity and not too complex structure for refuge (V).

However the presence of predators seems to be the important factor determining the choice of habitat (IV & V). The importance of submerged macrophytes as refuge might reduce in clay-turbid lakes (V). Perch and roach could use phytoplankton-induced turbidity as refuge when macrophytes disappear while they prefer low macrophyte coverage and plant volume infested when macrophytes are present (VI).

6. Implications of the results and future studies

The increasing eutrophication of northern temperate lakes during the last century has been one of the reasons for the decline of the commercially important fish stocks. A shift from salmoniformes to percids and a further shift to cyprinids with increasing eutrophication have been commonly observed (Hartmann & Nümann 1977, Jeppesen et al. 2000, Olin et al. 2002). Cyprinids such as roach, bream, and white bream are species that have been documented to profit from eutrophication (Persson et al. 1991, Olin et al. 2002). This is due to their effective feeding in turbid waters (Persson 1987), while perch need good light conditions for efficient foraging (Bergman 1988). The ability of cyprinids to utilise plant and detritus as a food resource (Persson 1983, Vinni et al. 2000), and their large capacity and flexibility in reproduction (Barthelmes 1983) are other reasons for their dominance in eutrophic lakes. In accordance with previous studies, the results here showed that the feeding of white bream was not affected by increasing clay turbidity. On the contrary to previous statements perch feeding was not affected by increasing clay turbidity, suggesting that perch may be able to cope with high turbidity levels as well as roach and white bream. Clay was used as turbidity in our experiments and turbidity in eutrophic lakes is mainly due to phytoplankton. Radke & Gaupisch (2005) showed that the predation success of perch was more affected by phytoplankton turbidity than by bentonite-induced turbidity however

the turbidity levels used were too low. Further experiments should be conducted to compare the effects of different types of turbidity on predation by percids and other cyprinids.

Fish may increase their swimming speed in order to make up the reduced search time caused by increasing turbidity (Aksnes & Giske 1993). In the long term, the effects of turbidity on feeding may lead to hindered growth rates of fish populations (Olin et al. 2002). Future studies could be conducted to clarify the effects of turbidity on the growth of different fish populations in clear and turbid lakes.

The regulation of the food web in pelagic aquatic ecosystems has received considerable interest for purposes such as improving water quality (Oksanen et al. 1981, Persson et al. 1992). Cascading effects in the food web are particularly strong in shallow lakes (e.g. Gulati et al. 1990, Jeppesen et al. 1997). The interactions between fish (piscivorous and planktivorous) and their potential prey (juvenile fish and zooplankton) play an important role in biomanipulation, a lake management method to improve the water quality of lakes (Shapiro et al. 1990, Mehner et al. 2002). Biomanipulation is done by manipulating the trophic levels, most commonly by removing planktivorous fish (Drenner & Hambright 1999). Also stocking of piscivorous fish is a common lake restoration method used (Skov et al. 2002). Cuker (1993) pointed out that the cascading trophic interactions in inorganic-turbid conditions may not follow the same pattern as in clear-water lakes. Predation by piscivorous fish can be affected by turbidity more severely compared to planktivorous fish (De Robertis et al. 2003) and not cascade down in turbid lakes. Horppila and Liljendahl-Nurminen (2005) reminded lake managers that predator-prey interactions in clay-turbid lakes might not cascade as predicted. The results of this thesis indicate that trophic interactions might differ in clay-turbid lakes compared to clear lakes, which should be considered in lake management as well.

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