Piscivore-prey fish interactions - consequences of changing optical environment

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Introduction

Predator-prey interactions are a primary structuring force in aquatic systems [1,2]. A change in the predator-prey interactions may cause a change in the strength of trophic cascades and even resulting in ecosystem shifts [3] and weakening of ecosystem resilience [4]. However, individual properties of predators and prey, as well as environmental conditions, may affect the relative strength of predator-prey interactions [5,6,7]. Most fish have a well-developed visual system and use it as their primary source of information [8], including detection of prey. Their foraging may be impaired by environmental changes affecting the efficiency of the visual system, such as reductions of water transparency [9,10,11] and ambient light intensity [12,13]. Reduced visual range have been shown to have a negative effect on several steps of the foraging cycle [14,15] as well as on prey behaviour and escape responses [16]. Piscivores and prey may differ in their response to degraded visibility conditions and, thus, the advantages/disadvantages may differ between piscivores and prey. This may, in turn, affect structural patterns in the fish community, for instance a change from a high abundance of piscivorous fish in clear-water lakes, to a dominance of cyprinids in more turbid and productive systems [17,18].

There are many different factors that could potentially affect the optical conditions in water, both man-induced and natural factors. Eutrophic lakes are characterised by a high biomass of phytoplankton, causing high turbidity and degraded visual conditions by scattering light and absorbing photosynthetically active wavelengths [19]. Many systems are also affected by high concentrations of suspended inorganic particles. The inorganic particles are either re-suspended from the bottom sediments during the windy season or enter the lake via run-off from terrestrial systems which are affected by precipitation but also changes in land use [20,21]. In addition, long-term monitoring data from aquatic systems show a dramatic increase in brown coloration over the last decades [22,23,24]. Several mechanisms have been proposed to explain the ongoing brownification, such as global warming, increased or changed patterns of precipitation [25,26] as well as decreased sulphur deposition [22,23].

All these factors that affect the optical conditions of the water are also affecting the lake ecosystem and its populations and individuals. To understand how lake ecosystems are affected by a change in the optical properties, we need to know more about both the effects on piscivorous fish and their prey on an individual level, but also how the interactions are affected between the different players. It is individual fish that face different situations, like changes in the optical environment, and make decision based on the information they obtain from the environment. Effects on the individual level will have secondary effects on the population dynamics and ecosystem functions, as all the parts within a lake ecosystem are linked.

This thesis deals with the interactions between prey and predators under visual constraints. Different predators with different foraging strategies combined with different prey species are tested against each other when the optical properties of the water are changing. If we can increase our understanding of how predator-prey interaction changes in response to degraded optical conditions this will in the end help us explain changes in different patterns and processes in lake ecosystems, for example growth patterns of fish and changes in fish community structure.

AIMS OF THE THESIS

The overall theme of this thesis is to investigate the effects of changes in the optical environment on piscivore-prey fish interactions in lake ecosystems. Changes in the environment may have either positive or negative effects on the foraging behaviour of the predator as well as on avoidance behaviours in the prey. By studying parts of the foraging cycle of the predator as well as prey behaviour, as the visual environment changes, we will gain more knowledge of what to expect as our aquatic systems change as an effect of eutrophication and brownification. Specific questions are:

- How will prey fish that judge predator threats based on visual cues compensate for the reduction in information in a detoriated optical environment? Will different visual inhibitors cause different effects on the predator response?

- How will different visual constraints affect predator-prey interactions between piscivorous fish and prey fish?

- What are the underlying mechanisms affecting prey selection in a piscivorus fish in clear and brown water? Can field patterns be explained by behavioural studies in the laboratory?

- Will the growth rate of prey and predatory fish change along a gradient of optical conditions (clear to heavily brown) in lakes?

METHODS

Study organisms

In the first study (paper **I**) I concentrated on the importance of visual versus chemical cues to determine predation threat, Crucian carp, *Carassius carassius*, was used as a model organism. Crucian carp are known to change both their morphology as well as their behaviour in response to chemical cues from predators [27,28].

In study **II** and **IV** I investigated the foraging behaviour and growth of pike, *Esox lucius*, a common piscivore in north temperate lakes. Pike is a visual predator with a sit-and-wait foraging strategy (Raat, 1988). Pike commonly feeds on roach, *Rutilus rutilus*, which was used as a prey species in study **II** and **III** and was also examined for growth pattern in study **IV**. Roach is a zooplanktivorous and benthivorous species that detect its prey on short distances and it has also been shown to be a superior forager in habitats with low complexity [29]. Other studies suggest that roach is successful in brown stained water [30]. Another commonly found species in brown water is pikeperch, *Sander lucioperca*, which is the piscivorous species studied in study **III**. In study **III**, I studied the selectivity of pikeperch when feeding on roach and perch, *Perca fluviatilis*, in the laboratory as well as in the field. Pikeperch is an active forager and are known to efficiently forage at low light intensities and in turbid/brown water [31],opposite from perch who depends on good light conditions.

Laboratory experiments

In study **I**, the focus was on how water colour (humic substances) and turbidity (clay and algae) affect fright responses (elicited by chemical cues from pike) in a freshwater fish, the crucian carp. The experiment was performed in a cylindrical arena (diameter 60cm) with a water depth of 5.5 cm; kept shallow to be able to track the fish. The visual range in the water was set to 0.4 meter. Crucian carp swimming activity were recorded, before and after pike chemical cue was added.

In two experiments (paper **II** and **III**) I focused on predator-prey interactions in different optical conditions. The visual range in the pike trials (paper **II**) were manipulated by adding turbid (clay and algae) or brown water to achieve the visual ranges of 0.25, 0.5, 1 and 2 meters. In the pikeperch experiment only brown water was used to reduce the optical properties to visual ranges of 0.25, 0.5 and 2 meters. The experimental set-up is shown in Figure 1.

In study **II** the experiment was divided into two parts: the first when only visual cues were available to the predator as roach was placed in a glass cylinder, and the second part where the roach was frees-swimming and pike and roach could freely interact and pike were allowed to use all senses. Behavioural parameters observed were reaction distance, attack distance of the predator and escape distance of the roach.

In the study with pikeperch (paper **III**), behavioural and prey selection experiments were conducted in a rectangular arena (2*.05*0.5m) with a water depth of 0.35 m. The water was manipulated with humic water to reduce the visibility in the water. For the prey selectivity experiments I used visual ranges of 0.25, 0.5 and 2m, but only 0.5 and 2m were used in the behavioural studies as behaviours could not be recorded at the lowest visual range. Prey selectivity was also studied for day and night conditions.

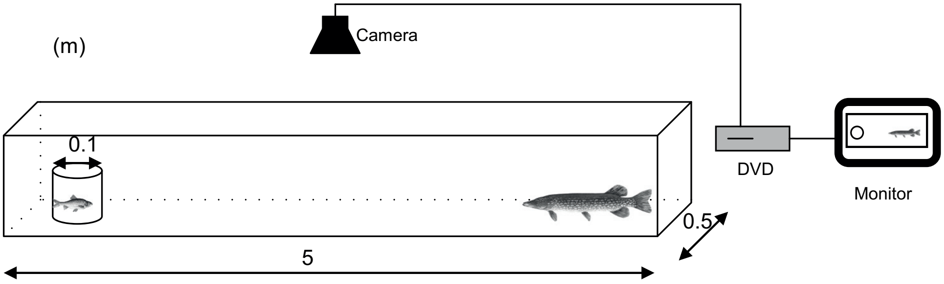

Fig. 1. Experimental set-up in laboratory experiment II and III.

Field

Two field studies were conducted. In study **III**, the focus was on prey selectivity in pikeperch in one clear and one brown water lake, during day and night. Pikeperch stomach content was analysed and compared to prey fish available in the lakes. In the multilake survey (paper **IV**) I investigated the somatic growth pattern of pike and roach in 12 lakes along a gradient from clear to heavily brown water. The survey was conducted in Southern Sweden (Skåne and Småland). The growth patterns were related to both biotic and abiotic factors, including fish abundance and absorbance of light.

RESULTS AND DISCUSSION

The visual environment

The optical conditions are constantly changing in the aquatic environment. Several factors are influencing the optical properties of water, including light availability and also inorganic and organic particles. Light intensity changes diurnally as well as seasonally, but can be considered to be constant over decades. Particles, on the other hand, are highly variable in nature due to both natural and human driven changes over the whole range of time scales. Over the last decades changes in both eutrophication [32,33] as well as brownification [22,24,25] has been observed. Turbidity varies seasonally driven by algal blooms and wind-driven suspension of lake sediment [34], but there could also be spatial variation in turbidity within a lake ecosystem [35]. Both turbidity and brown colouration are affecting the optical properties of lakes [36] resulting in reduced secchi depth [19,37] as well as changes in the light climate [38]. Turbidity is changing the optical properties by particles scattering and absorbing light [19], where light absorption is mainly caused by algae containing photopigments [39](Fig. 2). Humic matter is brown staining the water and absorbing light, especially in the UV-blue region [40], and gives optical conditions that are different from non-humic waters (Fig. 2).

In this thesis I have focused on different factors that affect the optical properties of water, including light intensity (day and night conditions), algae, clay and humic matter, and studied their affect on foraging in piscivorous fish as well as behavioural adaptations to recue predation risk in their prey. To be able to predict how ongoing climate changes as well as eutrophication and brownification will affect lake ecosystems and individual fish, it is of importance to test foraging mechanisms and prey behaviour under different optical properties.

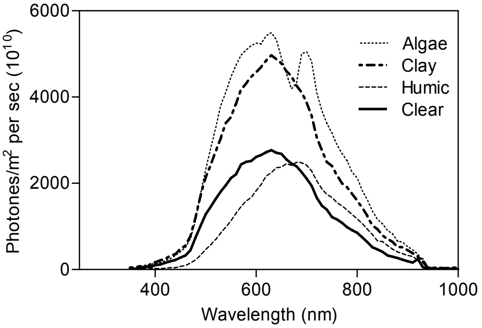

Figure 2. Spectral distribution of down welling light in clear water and water with algae, clay and humic matter measured at 5.5 cm depth.

Foraging cycle

The foraging of piscivorous fish can be described as a cycle with several outcomes: (1) the forager or (2) the prey interrupt the cycle, or (3) the forager will successfully catch the target prey. The cycle can be separated into different stages, including search, encounter, attack, capture and ingestion [41,42]. In this thesis I will focus on encounter, attack and capture stages. I will also bring in the perspectives of the prey into the foraging cycle since it is highly likely that interactions between the prey and the predator affect the probability of success in the different stages of the foraging cycle [43] (Fig. 3).

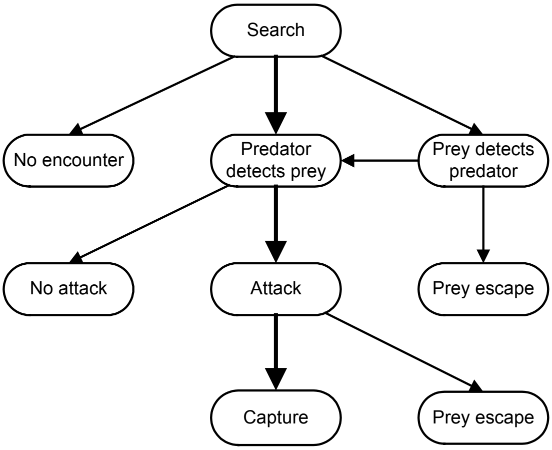

Figure 3. Flow chart of an interaction between a predator and a prey. The arrows represent the pathways in a foraging situation.

Search

Much of the time in a piscivorous fish life is designated to foraging. The foraging strategy could be either an active search strategy or a passive sit-and-wait strategy [44,45], where the decision of whether to be active or passive can be related to energy benefits and costs [45,46]. Pike is a typical sit-and-wait forager, waiting to detect a prey and attack from a hide-out [47]. When the optical properties in the environment are degraded, pike can no longer rely on visual foraging [48] and may then shift to active foraging [49]. Other species, such as pikeperch, are described to be active foragers searching for their prey in the pelagic zone [50], being less dependent on visual cues [51] and maintaining their activity in clear and turbid/brown water [52,Ranåker *et al.* unpublished data]. The activity pattern is also driven by diurnal changes, where some fish species are more night active [53] and others are day active [52]. In one experimental studies I looked at the activity pattern of pikeperch and found it to be more active (time spent moving) during night compared to during the day and twilight. However, the level of activity was not linked with the distance moved, which was highest in twilight conditions. The distance moved together with the optical properties of the water will affect the search efficiency (the area or volume that a predator can overview per unit of time) of the predator [54], and many fish species are known to optimize its foraging in dusk and dawn [51].

Encounter & reaction distance

The definition of an encounter is when the predator detects a prey, regardless if the prey is aware of the predator or not [55]. The encounter rate of a predator depends on prey density and search efficiency [41], where search efficiency in turn depends on the reaction distance of the predator (the distance between the predator and prey when the prey is detected) and swimming speed [9]. The reaction distance will be a more important determinant of search efficiency than swimming speed in stationary, sit-and-wait predators. Several studies have shown that stationary predators are negatively affected by changes in light intensity [15,56] and turbidity [9]. In the second study (paper **II**) I looked at foraging of pike at different visual ranges (0.25-2 meters) created by three different substances (algae, clay and brown water). We found the reaction distance of pike to correlate with the visual condition in the water (Fig. 4), and we also found the reaction distance to be context dependent. Reaction distance was longer in brown water compared to algae water. The changes in reaction distance are probably due to changes in the scattering of light, affecting contrast of the prey against the background [57]. Effects of scattering are more pronounced in the turbid waters resulting in stronger effects from algae on reaction distance than brown water. The effect of brown water on reaction distance was also tested in another piscivore, pikeperch, and here the effect of the decreasing optical properties showed to cause less of an effect on foraging [Ranåker *et al.* unpublished data] compared to pike (Fig. 4). The differences between pike and pikeperch may be due to their different foraging strategies and will be discussed more in the section **Differences among predator species**.

Attack/Strike

The third step of the foraging cycle is the attack/strike of the piscivorous fish. The strike can be categorized into different mechanical types based on the movement pattern of the accelerating predator and the acceleration [58]. During the strike the fish can either change their direction in the attack sequence, where the piscivore re-orient towards the prey or make no directional changes and manoeuvre head-on towards the prey [59,60]. Which attack strategy the predator select can be of importance as the attacks can account for up to 80 % of the total energy spent by

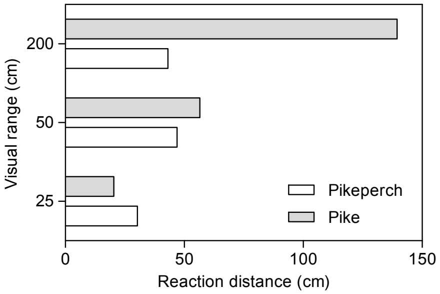

Figure 4. Reaction distance of pike and pikeperch to roach in brown water with three visual ranges.

the predator [61]. In two studies (paper **II** and **III**) I have investigated the number of strikes as well as strike distance of both pike and pikeperch towards the prey. Since pike and pikeperch have different foraging strategies (pike: sit-and wait; pikeperch: pursuit strikes) and different strike sequences it is of interest to see how they will be affected by the reduced visual range, especially since their reaction distance were affected in different ways by the optical condition (see *encounter & reaction distance*). We found that pike strike distance was unaffected by visual range, which is probably a result of the sit-and-wait foraging strategy in pike where attack is initiated at short prey distances [58,59]. In our experiment the shortest visual range was 25cm and hence greater than the approximate strike distance range, why we suggest this as a mechanism behind that strike distances were never affected by visibility. We also found that pikeperch strike distance was longer in 0.5 than in 2 meters visual range. Pikeperch is active during the attack phase and chase its prey [62]. In limited visual condition, the prey can easily escape out from the reaction distance [5,63] of the pikeperch, which may result in enhanced attack distance.

Capture

The foraging cycle ends when the piscivorous fish captures the prey. The capture success of the piscivorous fish is affected by several biotic and abiotic components, such as defence [64], size of the prey [65] as well as the optical environment [66]. Prey defence strategies will be described in the section **Predator avoidance**.

In pikeperch, we found that capture success when attacking perch was significantly lower when the visual range in the water was reduced (paper **III**). This is in line with a study by Zamor and Gossman [66], also showing negative relationship between the optical environment and capture success. The increase in number of strikes as visual environments was degraded may be due to a change in foraging strategy increasing the number of interactions [67]. However, the capture success on roach increased with reduced optical conditions, which may be due to prey behavioural changes (see **Predator avoidance**).

Selectivity

Selectivity is defined as any difference in prey type composition in the predator diet compared to composition of available prey types in the environment [68,69]. Several studies indicate that piscivorous fish are selective foragers as their diet do not reflect prey availability [68,70, Paper **III**]. In paper **III** we compare prey selection in the field and in an experiment. In our field study we evaluate if pikeperch show selectivity for perch and/or roach in one clear and one brown water lake. Perch were the selected prey item in both lakes during day, whereas roach was selected during night, the same pattern was found in the experimental selectivity study. The behavioural studies showed no significant difference among prey in pikeperch number of interest, or number of attacks, i.e. active choice is not a major contributor to pikeperch selectivity. Instead, prey selectivity in pikeperch seems to be a result of processes at later stages in the foraging cycle, i.e. at the capture stage. We found that capture success was affected by both which prey species was attacked and the visual range in the water. In the laboratory experiment we found a 100% capture success for pikeperch foraging on perch in clear water and a 0% capture success when foraging on roach, which thus explain why pikeperch show selectivity for perch during day. Pikeperch attack distances were always shorter than the measured escape distances of roach in clear water, i.e. roach avoid predation by initiating an early escape response at distances that are outside the distance where pikeperch initiate their attacks. However, as the visual range or light intensity decreased, roach change their behaviour (see **Predator avoidance**) resulting in that pikeperch are able to catch roach.

Predator avoidance

Fish living under predation pressure have evolved both behavioural and morphological defences to reduce the risk of predation. Two common morphological adaptations found in prey fishes are (1) Spiny fin rays (perch) and (2) deep- and shallow-bodied fish (Crucian carp). Prey fish having spiny fin rays are less selected by predators than prey fish with soft ray fins [64,71] as the spiny fins makes the prey more difficult to catch and swallow [71] and, further, spines can injure the predator [64].

Another adaptation commonly found in prey fish is behavioural changes, such as changes in activity levels [72,73] and shoal formation [74]. A prey in motion is easier to detect by a predator than an inactive prey and it has been shown that prey in fear of predation commonly reduce their activity or freeze [28,75]. In our study (paper **I**) where we exposed a crucian carp to chemical cues from pike we found that the reduction in activity in response to predator cues was dependent on visual range and the substance reducing the optical properties in the water (Paper **I**). The reduced activity can lead to reduced predation on the crucian carp as the level of activity has shown to affect the reaction distance of visually foraging fish [76,77]. In paper **III** we also observed that perch were less active in the presence of the predator. A passive strategy (lowered activity) can be considered a cost efficient strategy as there is an cost of escaping [73,78] and therefore, animals do not necessarily escape as they detect a predator [5]. However, there seem to be an escape distance threshold where a delayed escape results in increased foraging success of the predator and mortality for perch (paper **III**).

Roach, on the other hand, formed tight schools and actively avoided to enter the attack distance zone of the pikeperch. Experimental works on escape and reaction distance of prey show conflicting results, where for example Abrahams [79] found longer reaction distance for solitary than shoaling fish, Godin and Morgan [80] found no effect of group size and Semeniuk and Dill [81] found longer reaction distance for prey fish in shoals than solitary fish. Other studies show a shoal confusion effect [82], where some species suffer confusion effect with increasing shoal size, whereas other species do not seem to be affected by shoal size [62]. In paper **III** I showed that roach was successful in clear water. In this treatment the roach were shoaling and actively avoided the pikeperch. However, shoaling depends on good optical condition as vision is a key component in shoal formation [83]. When the optical condition was reduced either by brown colouration of the water or light, the roach shoal split up [Ranåker *et al.* unpublished data] (Fig. 5) and this probably resulted in a less efficient anti-predator defence as roach became the main prey item at low visual ranges and in dark environments (paper **III**).

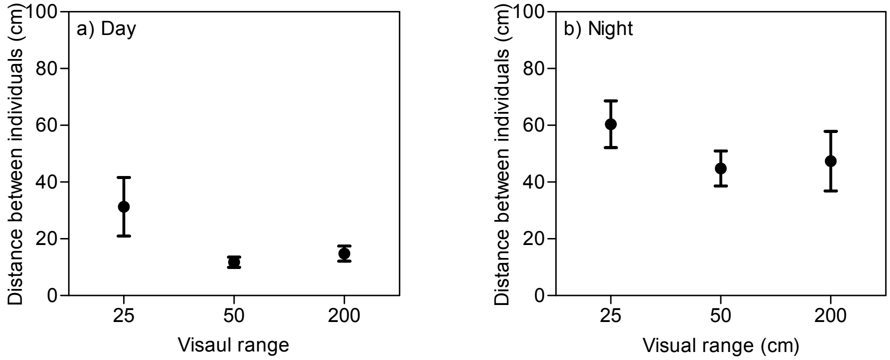

Figure 5. Shoal. Mean distance between two roach individuals at different visual range in a) day light conditions and b) night conditions.

Predator-prey interactions

Most studies dealing with foraging cycle components have focused on either predator or prey behaviour [84]. But we should not forget that the predation event can be disrupted at any step of the foraging cycle, due to the predator, the prey or both players. When observations only are made on one of the two players, you might not get the whole picture. In my studies I have focused on both the prey and the predator, and thereby gained information why and where interactions between the two players take place.

In the studies I have found that the predator-prey interactions change with changes in the optical environment and depend on both the predator and the prey. This is important knowledge enabling us to make further predictions of the ongoing brownification as well as eutrophication. For example, we observed changes in the strike distance of the pike and escape distance of the roach as the water colour increased. At high and intermediate visual range the roach's escape distance were longer than the strike distance of the pike, but as visual range in the water decreased the escape distance of the roach was dramatically reduced and ended up within the strike distance of the predator. An overlap like this should increase interactions between the prey and the predator and increase the probability of successful attack. Further, there are differences among prey species. Roach that manage to stay outside the strike zone of the pikeperch is never captured, whereas perch, which is passive and have short escape distances will be captured in 100% of the trials in good optical condition. At intermediate visual range the escape distance of the perch and roach are similar and this results in that pikeperch capture success becomes equal for the two species.

Visual cues and alternative senses

Most fish are considered to use their vision to gain reliant information for decision making [85], but when the optical environment is limited the fish may alter their use of vision and instead increase their use of other senses [86]. Thus, a limited visual field may cause a sensory compensation towards use of chemical or mechanical information [86, Paper **I**, Paper **II**]. Chemical information are known to influence both the morphology [27] as well as behaviour [87] of prey fish. The sensory compensation model suggests that vision is the primary source of information, and that other cues are used only when the optical conditions in water reduces the reliability of visual information [86]. We observed behavioural changes in crucian carp as it was exposed for predation threat in form of cues from a predator. The response was however context-dependent (paper **I**), with

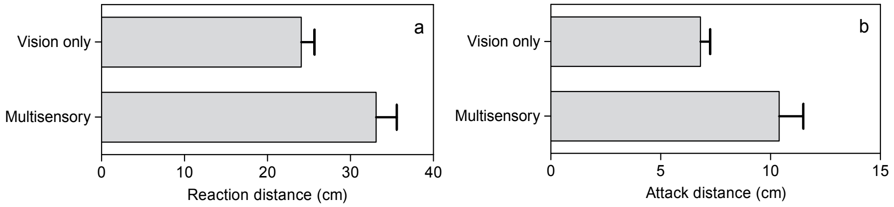

Figure 6. Reaction distance (a) at 0.25cm visual range, and attack distance (b) at 0.25, 0.5, 1 and 2m of pike when they only can use visual information (vision only) and when they can use all their senses (multisensory).

significantly decreased activity in waters with deteriorated visibility, whereas there was no response in activity to predator cues in clear water. Visual information seem to be the primary information source for the crucian carp, but as the visual information is limited then alternative senses are used.

Also a visual predator use alternative senses in decision making, when alternative cue is available [88]. We observed that pike foraging on roach (paper **II**) in an environment with degraded visual environment enhance their reaction distance (at visual range: 0.25 cm), as well as strike distance (for all visual ranges), when they were able to use all senses compared to when they only could use visual information (Fig. 6a). Strike of the pike is always within a short distance, and here the multisensory use seems to increase the strike distance, independent on the visual condition in the water (fig. 6b). The pike seem to benefit from multisensory cues at close distance foraging, but at longer distances (≥0.5m) it seems as vision is the primary source of information. The decreased strike distances when pike was limited to only visual information are probably due to a reduction in assessment capacity in pike when to make the final decision to strike. When prey is free swimming, pike are able to use multiple senses, including the sideline and chemosensory systems, additively when foraging [89]. The enhanced ability to determine the position of a prey by using multiple senses may allow for a longer strike distance, which should render a relative benefit to pike in extremely deteriorated visibility conditions where visibility is shorter than prey escape distances.

Differences among predator species

To reflect on ongoing situations in natural systems, recent studies have highlighted the importance of evaluating multiple predators simultaneously [90,91,92]. However, the outcome of such studies may also depend on ecosystem-specific conditions, such as the optical environment [91]. For example, as the optical environment changes, predators may alter their foraging strategy [67]. In our field and experimental studies we have evaluated predators foraging under visual constraints. Earlier studies show that ambush predator capture more prey than cruising predators in clear water and the opposite pattern is found in turbid waters [91,93]. We found a similar pattern with our ambush predator pike and cruising predator pikeperch, further, we found the foraging mechanisms and prey behaviour to interfere with the foraging success. The foraging strategy of pike is not adapted for a limited visual field as they are passive, sit-and-wait predators, and rely on activity of the prey species. Reduced visual properties showed to have minor negative effects on the reaction distance of pikeperch, although we also observe that pikeperch only were able to catch perch in good optical condition whereas they caught both perch and roach as the optical condition was reduced. Thus, limited optical condition seem to be beneficial for pikeperch [94] as it increases the diversity and biomass of prey species available. This may explain why pikeperch are superior in brown and turbid lakes [95,96], where the pike seem to suffer both in growth [97](paper **IV**) and biomass [17].

Growth pattern

All the other sections describe how the optical properties will affect foraging in piscivores as well as predator avoidance in their prey fish. The results provided from these studies gives a hint on how the individual fish growth rate pattern will be affected by changes in their optical environment. In paper **IV** we evaluated the growth of individual pike and roach in lakes along a gradient from clear to heavily brown stained water and found that both pike and roach growth are negatively affected by brownification. The fish densities in the studied lakes were not correlated with colouration. The negative growth pattern found in pike was enhanced with age. The reduced growth of pike is likely to be an effect of the reduced reaction distance (paper **II**), affecting the encounter rate, and also the consumption rate. The reduced roach growth may be due to food availability, which has been shown to decrease with increasing colouration [98]. Besides zooplankton, macroinvertebrates is an important food source for roach [99], but with increasing brown colouration the macrophytes (the main habitat for the macroinvertebrate) decrease in complexity and biomass [100], which may have a negative effect on the abundance of macroinvertebrates.

Depending on which species you study within a lake ecosystem you will find that different growth related abiotic and biotic parameters will affect the growth. Differences in the growth and the power of parameters will change along with age of the species.

Conclusions and future perspectives

In the studies I observed two different behavioural defences against predators. Both crucian carp and perch decreased their activity when exposed to pike chemical or visual cue. However, the behavioural response elicited by the chemical cue was context dependent, i.e. crucian carp only reacted to the cue if information from visual senses was limited (turbid or brown water). To stay inactive reduce the risk for a prey to be detected by a predator. Another behavioural response to predation threat is shoaling as shown in roach, a common prey fish, that group into shoals to limit predation risk.

The interaction between the predator and prey fish was influenced by optical conditions. Reaction distance of pike, which is a sit- and wait-forager, showed to be negatively affected by reduced visual conditions. The reaction distance and attack distance of pike and escape distance of roach was also context dependent, where brown water increased the reaction and attack distance in pike and reduced the escape distance in roach. This resulted in an overlap in attack and escape distance, which may have positive effects on the capture success of pike. Pikeperch, which is an active forager, was less affected by changes of the visual conditions in the water. However, pikeperch was indirectly affected by changing optical conditions through a change in prey behaviour.

Pikeperch showed a strong preference for perch under good optical conditions, but shifted their food preference to roach in poor optical conditions. The underlying mechanism to this pattern was observed in behavioural studies. Roach escaped long before the pikeperch initiated an attack, whereas perch was inactive which allowed pikeperch to approach and successfully attack. In poor optical conditions roach shoals were splitting up and roach escape distance was strongly reduced, which increased the foraging success of pikeperch resulting in that both roach and perch were included in the diet.

These changes in the predator-prey interactions may explain some of the changes in fish growth rate observed in lakes along a gradient of brown colouration. Here, we found that the growth rate of pike and roach were reduced in browner lakes. Foraging of pike will be negatively affected by the brown colouration, which may result in reduced prey consumption and, hence, reduced growth rates. Roach growth will probably be more affected by prey availability, which may be low in brown water lakes due to the reduced productivity associated with brownification.

In this thesis I show that different fish species react differently towards each other in brown compared to turbid waters, even though the human visual range is the same. In order to understand the underlying mechanisms behind the detection of both prey and predators under different visual constraints, it is essential to understand exactly how different constraints affect object detection. Scattering by particles, as in turbid water, should have different effects to changes in wavelength spectrum, as in brown water. Further, the colour and reflectance of the objects, i.e. the fish, themselves should affect the contrast to the background. An increased understanding of adaptations to avoid being detected in different fish species, and why they detect each other and on what distance, might help us to explain predator-prey interactions in more detail and the implications for processes at the population, community and ecosystem levels.

The change in species composition leads me into another direction, an extension of the outcome from this thesis. In lakes undergoing brownification a change in fish biomass, but also composition has been observed. As fish species composition has strong effects down the food chain through cascading trophic interactions this may have remedies for the whole lake ecosystem. A double trouble is that pikeperch is often stocked into these systems as they are a superior competitor in lakes with low optical properties and seem to be able outcompete pike and other important fish species for the ecosystem. It would be of great interests to do a long term study controlling for both brownification and pikeperch stocking and observe how the lake ecosystem changes.

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