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2012

Citation for published version (APA):
Jönsson, M. (2012). *Fish foraging under visual constraints*. [Doctoral Thesis (compilation), Department of Biology]. Department of Biology, Lund University.

Total number of authors:
1

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AKADEMISK AVHANDLING
som för avläggande av filosofie doktorsexamen vid
naturvetenskapliga fakulteten, Lunds universitet kommer att
offentligen försvaras i Blå Hallen, Ekologihuset, Sölvegatan 37, Lund,
fredagen den 27 april 2012 kl 9:30

Fakultetens opponent: Professor Peter Eklöv, Avdelningen för limnologi,
Evolutionsbiologiskt Centrum, EBC, Uppsala universitet, Sverige

Avhandlingen kommer att försvaras på engelska

Dissertation
Lund 2012

Organization
LUND UNIVERSITY

Department of Biology
Aquatic Ecology
S-223 62 Lund
Sweden

Document name
DOCTORAL DISSERTATION

Date of issue
14 March 2012

Sponsoring organization
Swedish Research Council FORMAS

Author(s)
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Title and subtitle

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Abstract

Visual conditions are changing in several different ways. Some lakes are getting turbid due to eutrophication or erosion while others are getting browner due to brownification. These two types of visual degradation results in completely different optical properties of lakes. Turbid water scatter light which degrades image quality severely while brown coloured humic water mainly absorb light making the aquatic environment darker.

In juvenile fish, the effects seem to be similar between turbid and humic water where foraging of planktivorous life stages are largely unaffected. However, prey selectivity in juvenile fish may change as red carotenoid pigmentation in copepod zooplankton make them more conspicuous in turbid water while transparent copepods are selected by the fish in humic water. The pigments, that are usually used for UV-protection in clear water, may therefore make the pigmented copepod cryptic in humic water, explaining the presence of the pigments even in brown waters where UV-radiation is very low.

Piscivorous juvenile fish experience negative effects of visual degradation, including reduced reaction distance which reduces the search efficiency and encounter rate for the predator. Juvenile pike (Esox lucius) are able to counteract the reduced encounter rate with increased attack rate and thereby probably also higher foraging effort. This increase in foraging effort when foraging on fish prey may reduce the benefit of ontogenetic diet switches and thereby have consequences for growth and recruitment in fish populations.

Foraging in adult fish depend heavily on visual conditions. For adult fish, image quality is important, resulting in that prey size selectivity collapses completely in turbid water. In clear water pike consistently selects small prey to reduce handling time to a minimum. This selectivity for small prey are maintained in brown humic water. Lost selectivity in turbid water and thereby capture of larger prey than necessary, increases the handling time of prey, and thereby the exposure of pike to cannibalistic and cleptoparasitic conspecifics. However, the most pronounced foraging cycle effect of visual degradation is the reduced reaction distance that lowers the search efficiency of the predator and thereby possibly the encounter rate with prey. Decreased encounter rates was however not counteracted by increased search activity. The importance of the visual conditions for the encounter rate is also implied when growth rate of perch (Perca fluviatilis) was evaluated before and after biomanioulation in Lake Finjasjön. A 10-fold decrease in prey density after biomanipulation is completely counteracted by improved visual conditions where Secchi depth increased from 0.35 m before to 1.16 m after biomanipulaton. This resulted in increased growth in the predator, probably due to increased encounter rate, despite the 10-fold decrease in prey density.

Key words: Turbidity; visual foraging; brownification; piscivore; planktivore.

Classification system and/or index termes (if any):

Supplementary bibliographical information:

Language
English

ISSN and key title:

ISBN
978-91-7473-299-3

Recipient's notes

Number of pages
100

Price

Security classification

Distribution by (name and address)

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DOKUMENTDATABLAD enl SIS 61 41 21

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Layout: Mikael Jönsson
Proof reading: Mikael Jönsson
Printed by Mediatryck, Lund

ISBN 978-91-7473-299-3

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Sammanfattning på svenska

De optiska egenskaperna i våra sjöar och vattendrag förändras kontinuerligt. Näringsrika sjöar blir grumliga genom algblomningar och erosion gör vattnet grumligt av lerpartiklar. De senaste årtiondena vattnet också blivit brunare genom att mer humusämnen läcker från omkringliggande mark. Både grumligt och humöst brunt vatten försämrar fiskens siktförhållande, men det sker genom helt olika mekanismer. Grumligt vatten innehåller partiklar som sprider ljuset vilket försämrar kontrasten och sänker kvaliteten på den visuella informationen. Humöst vatten är brunfärgat av lösta organiska ämnen som absorberar ljuset istället för att sprida det. Absorptionen gör miljön under vattnet mörkare men bibehåller kvaliteten i den visuella informationen.

För juvenil mört (*Rutilus rutilus*) och gädda (*Esox lucius*) är effekterna av grumligt och brunt vatten likartade så länge de äter plankton. Däremot påverkas bytesselektiviteten av vattnets optiska egenskaper. I grumligt vatten föredrar juvenil gädda att äta rödpigmenterade copepoder, medan de i brunt vatten föredrar genomskinliga copepoder. Det röda pigmentet, som generellt används som skydd mot skadlig UV-strålning, fungerar som kamouflage i brunt vatten. Detta kan förklara varför copepoder har kvar pigmentet i en miljö som har mycket låg UV-strålning eftersom UV-strålning snabbt absorberas av det humösa vattnet.

Juvenil gädda som äter annan fisk påverkas negativt av turbiditet och brunt vatten genom att detektionsavståndet till byten minskar kraftigt. Detta ger dem sämre födosökseffektivitet och de träffar mer sällan på lämpliga byten. Gäddan motverkar detta genom att öka sin benägenhet att attackera påträffade byten. Det kan dock leda till en ökad energiåtgång som i förlängningen kan få konsekvenser för tillväxt och rekrytering.

Större gäddor påverkas kraftigt av försämrade siktförhållanden och kvaliteten på den visuella informationen är mycket viktig. I klart vatten föredrar gäddor att äta småfisk för att snabbt kunna svälja bytet utan risk att bli upptäckta av andra större gäddor. I grumligt vatten, med låg visuell kvalitet, bryter dock denna bytesstorleksselektivitet samman och gäddan blir tvungen att attackera byten

som inte är optimala. I brunt vatten däremot, bibehålls selektiviteten för småfisk eftersom kvaliteten på den visuella informationen bibehålls. Det som dock påverkar gäddan mest är att detektionsavståndet till bytena minskar i både grumlig och humöst vatten vilket gör att deras födosökseffektivitet också minskar och de träffar på färre potentiella byten. Detta skull kunna motverkas genom att gäddan simmar mer och därigenom träffar på fler byten men så är inte fallet.

Att siktförhållandena är viktiga för rovfisk blir tydligt när tillväxt hos abborre (*Perca fluviatilis*) analyseras före och efter biomanipulering av Finjasjön. Efter biomanipulationen hade bytestätheten för abborren minskat till 1/10 av vad den var före biomanipulationen. Däremot har sikten i vattnet förbättrats från 0,35 meter till 1,16 meter efter biomanipulationen. Denna förbättring av siktförhållandena i vattnet motverkar helt minskningen i bytestäthet, och ger till och med ökad tillväxt hos abborren, troligtvis genom att abborren träffar på fler byten eftersom sikten är bättre och detektionsavståndet längre.

BACKGROUND

For long, it was assumed that the different trophic levels that constitute the biotic part of the ecosystem was regulated by the amount of available resources the bottom-up theory. According to this theory, high nutrient input stimulates primary production, which in turn supports primary consumers and predators. However, it was later discovered that lower trophic levels may not only be limited by resource availability, but also by their consumers. By feeding on lower trophic levels, predators keep prey at lower densities than if predators were absent; the top-down theory (Hairston, Smith & Slobodkin 1960; Carpenter, Kitchell & Hodgson 1985; Northcote 1988). In the footsteps of this theory, many systems have been suggested to be top-down controlled, acknowledging the importance of predators in the dynamics of entire ecosystems (Carpenter et al. 2010). By affecting the trophic level below, predators induce trophic cascades that ripple through the food web with far reaching consequences, not only for the closest trophic levels. This has been implemented in applied restoration projects where these trophic links have been used to manipulate disturbed systems and push them to a more desirable state (Shapiro, Lamarra & Lynch 1975; Hansson et al. 1998; Søndergaard et al. 2007). A good example of this is the numerous biomanipulations of lakes carried out throughout the world where one or two trophic levels, usually fish, are manipulated with consequences for the primary producers several steps down the food chain (Shapiro, Lamarra & Lynch 1975; Søndergaard et al. 2007). More recently, this cascade has also been shown to occur even if the predator does not consume any prey. This is known as a "behavioural cascade" where the mere presence of a predator alters the behaviour of prey, with further effects down the food chain (Stich & Lampert 1981; Werner et al. 1983; Romare & Hansson 2003; Lehtiniemi, Engstrom-Ost & Viitasalo 2005; Van de Meutter, De Meester & Stoks 2005). This highlights the crucial importance of consumers in limiting and controlling organisms at lower tropic levels, but it also suggests that any factor, biotic or abiotic, that affects the foraging performance of consumers may cascade and affect the entire ecosystem.

The most important consumers in aquatic ecosystems are typically piscivorous and planktivorous fish. These fish use an array of sensory cues to explore their environment, but most are visually oriented (Guthrie & Muntz 1993) meaning that they mainly use visual cues for locating their prey. Degrading the visual conditions for these predators may alter their ability to find and consume prey, but at the same time risk assessment in their prey may be affected as less visual information is available to them. These are factors that are crucial for the success of both predators and prey and for the strength of direct and behavioural cascades, mediated through reductions in the visual information.

This thesis is about the effects of visual conditions on foraging in visually oriented fish and particularly if different types of visual degradation have different effects. It further explores how fish are affected at different developmental stages throughout their life as success during juvenile stages govern the recruitment of fish to larger size classes. Visual degradation is also predicted to affect foraging differently for different prey sizes and fish generally change prey size/type preference during early ontogeny.

Visual detection in fish: the basics

Visual detection in fish have been extensively studied, both empirically (Vinyard & O'brien 1976; Gregory & Northcote 1993; Miner & Stein 1996; Utne-Palm 2002; Mazur & Beauchamp 2003) and theoretically (Aksnes & Giske 1993; Beauchamp et al. 1999). To detect an object, a critical threshold contrast between the object and the background has to be reached (Equation 1). This inherent contrast (C) between an object and its background is expressed as:

$$C = \frac{\left(E_p - E_b\right)}{E_b} \tag{1}$$

where E_b is background radiance and E_p is the radiance of the object (Hinshaw 1985; Utne-Palm 1999). However, detection is not only depending on the difference in the level of radiance between the object and the background (C), but also on the distance to the object and properties of the water. This parameter is called the apparent contrast (C_a, equation 2), which decreases with an increase in beam attenuation coefficient (c) and increasing distance (x) to the object (Utne-Palm 2002).

$$C_a = C^{-cx} \tag{2}$$

The beam attenuation coefficient describes the optical properties of water, and is the sum of the amount of light removed by scattering and absorption. This concept has been further developed to include more physiologically relevant parameters (Aksnes & Giske 1993) where a critical energy change in the retina of the fish (ΔS_r) can be used instead of the inherent contrast (Equation 3).

$$\Delta S_r \leq C_r A_{pr} E_{br} \tag{3}$$

where C_r is the retinal contrast, A_{pr} is the size of the retinal projection of the object and E_{br} is the retinal background light level. In order to reach the critical energy change value (ΔS_r) one can either increase retinal contrast (C_r), retinal background light level (E_{br}) or size of the retinal projection (A_{pr}). The size of the retinal projection in turn depends on both size of the object and the distance to the object (*x*), so increases in A_{pr} can be achieved either by increasing object size or decreasing distance to object, or both. Hence, detection of an object in the water by a fish depends on the difference in contrast between the object and its background (C_r and E_{br}), which in turn is affected by the optical properties of the water and the size of and distance to the object (A_{pr}). It is clear that contrast is important for detecting objects (Lythgoe 1979; Hinshaw 1985), and as optical characteristics of the water can be assumed to affect contrast, there are also potential effects of visual degradation on foraging in fish.

Visual conditions

Visual degradation has for a long time been acknowledged as a major environmental problem (Shapiro, Lamarra & Lynch 1975; Lind 2003; Søndergaard et al. 2007). However, this is maybe not because of the visual effects *per se*, but for other reasons. Increasing erosion has caused inorganic particles from the surrounding soils to be suspended in the water (Lind 2003) and eutrophication has increased algal growth rates and thereby increased turbidity in the water (Anderson, Glibert & Burkholder 2002). However, during recent decades another visually degrading agent has been observed to increase; humic substances or dissolved organic matter (DOM). Humic substances causes lakes to become more brown coloured, a process called “brownification” (Graneli 2012), and during the last 40 years the concentration of humic substances in water on the Northern hemisphere has increased steadily (Hongve, Riise & Kristiansen 2004; Monteith et al. 2007; Erlandsson et al. 2008). These humic substances are mainly a product of decomposition of plant material from the surrounding landscape which is transported with surface runoff to lakes and streams (Roulet & Moore 2006). While turbidity is caused by relatively large particles in the water, e.g. clay or phytoplankton, the brown humic substances are dissolved in the water, giving brown water completely different optical characteristics compared to turbid water. In the following paragraphs I will discuss these differences between clear water,

water that is turbid due to algae or clay, and water coloured brown by humic substances. When I write “turbid”, I refer to both algal and clay turbid water as they have very similar characteristics and I refer to water coloured brown by humic substances as “brown or humic water”.

Both turbid and humic water makes the under-water conditions darker, meaning that the light intensity in the water column is reduced compared to clear water conditions. However, the causes of this reduction in light intensity differ and the differences are also important from an image quality point of view. The basis of this discussion is the size of the particles. Clay and algae are rather large particles that are suspended in the water while the humic substances in brown water are molecules that are dissolved in the water and much smaller than the suspended particles. When light travels through turbid water and hits a particle it will be scattered, the degree of which depends on the size of the particle and the wavelength of the light. Large particles scatter most wavelengths of light while smaller particles scatter mostly shorter wavelengths. When sunlight enters the water from above it hits particles in the water and is scattered, and as some light is scattered upwards, less light is going downwards, making deeper water layers darker through shading. Further, light is scattered in all possible directions which results in that the light that reaches the sediment has probably been scattered several times. This is the same for image forming light, light that travels between an object and the eye of an observer, i.e. light that is reflected from the surface of an object and which we register when we see it. When the image-forming light changes direction upon scattering, it means that it will not end up at the correct place on the retina where the image is formed, but will be slightly displaced, decreasing the contrast between the object and the background. When the majority of the light that is supposed to make up an image has changed its direction you end up with a blurry image where exact outlines of objects and textures are difficult to make out. This contrast reduction is the predominant mechanism for visual degradation in turbid water. However, algae also have selective absorption in the wavelengths used for photosynthesis, photosynthetically active radiation (PAR), and thereby reduce the light intensity in the water. However, this absorption is relatively small compared to the scattering (Figure 1) and also compared to the absorbing potential of brown water (Figure 2).

The humic substances in brown water are rather large molecules, but still they are much smaller than phytoplankton and clay particles. Also, their molecular structure can be altered when exposed to light. When light hits the humic substances it is absorbed as the energy in the light is used to change the molecular structure and degrade the humic substances (Backlund 1992). The energy that

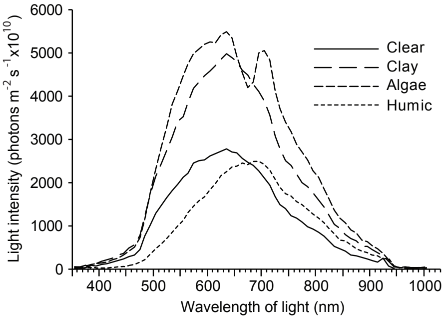

Figure 1. Level of scattering, measured as the amount of light reaching a light senson at a 15 degree angle from the bottom of an aquaria. High light intensity indicates high scattering and low intensity indicates that light pass through the water undisturbed.

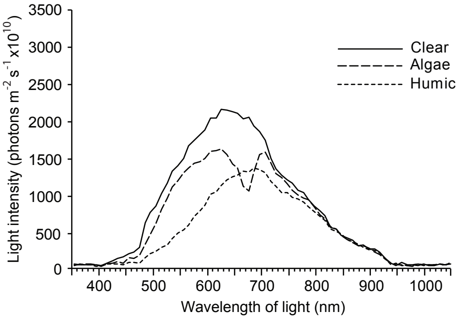

Figure 2. Light intensity masured at the bottom of an aquaria with the sensor directed towards the light source. High intensity indicates that most of the light that enters the water reaches the sensor while low intensities indicate that light is attenuated trough scattering and absorbtion.

is required to induce these molecular changes is taken from the light and it is therefore absorbed. Humic water has a general absorption of most wavelengths, but the attenuation of high energy light (short wavelength, UV, violet to blue) is stronger than low energy light (long wavelength, red to infrared, Davies-Colley & Vant 1987). In humic water, UV-radiation is therefore attenuated fast and only present close to the surface of the water. As the visual system of some fish has been shown to exhibit sensitivity in the UV part of the spectra (Rick & Bakker 2008; Tada, Altun & Yokoyama 2009), this adds to the optical differences between turbid and brown colured humic water. Water with a low degree of scattering have the potential for retaining contrast between the background and the object giving humic water completely different optical properties than turbid water. The visual conditions are important for visual predators but the question is how reduced detection ability and image quality affects the actual foraging event for a predator and if turbid and humic water have similar effects despite the large optical differences.

Foraging

Foraging consists of a series of stages that have to be completed for a predator to successfully consume a prey. These stages are called foraging cycle components and are part of the foraging cycle (Figure 3), modified from (Endler 1991). The cycle starts with the search component, a predator has to search in order to find prey. Once the prey is found an encounter occurs, which is the second component. When the encounter has occurred the predator may decide to attack, which is the attack component. If the attack is successful the predator enters the capture component, which is followed by the ingestion and digestion components (Figure 3). The foraging cycle is only completed when a prey is fully digested by the predator and it may be aborted at any stage in the cycle. For prey it is important to abort the cycle as early as possible as the risk of injury and mortality increases as the cycle progresses. It may be aborted early if a prey can avoid being detected by the predator or if it can avoid being attacked after detection. The prey may also escape after capture or simply be too large to swallow. There are many more ways to abort the cycle and by dividing the foraging event into different foraging cycle components we can pinpoint how foraging is affected by, for instance, changes in visual conditions. The concept of foraging-cycle components is central to the rest of this thesis and discussions are based on this. The possible effects of the visual conditions on the separate components are discussed under the papers that deal with the specific components and the papers are hereafter referred to using their roman numbers.

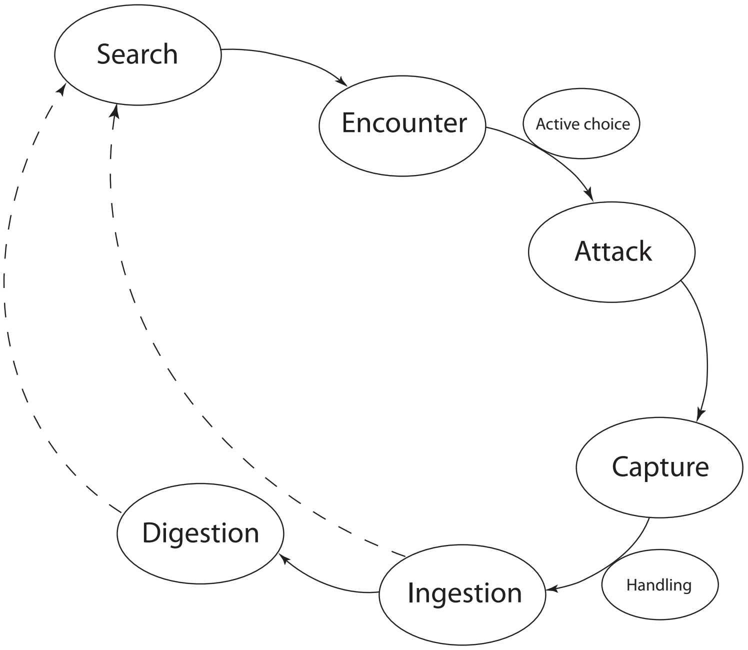

Figure 3. The components of the foraging cycle, including search, encounter, the choice to attack or not, capture, handling, ingestion and digestion, modified from Endler (1991).

AIMS OF THE THESIS

The effects of turbid water has previously been evaluated for different fish species with different foraging modes and prey types (Vinyard & O'brien 1976; Reid, Fox & Whillans 1999; Utne-Palm 2002; De Robertis et al. 2003; Mazur & Beauchamp 2003). However, the effects of humic substances colouring the water brown are very scarcely discussed in the literature. Papers describing population level effects of brown water are present (Karlsson et al. 2009; Horppila et al. 2010) and some very recent papers deal with planktivorous foraging in fish in brown water (Horppila et al. 2011; Estlander et al. 2012). But mechanistic studies on piscivorous foraging in brown water is largely lacking. As turbid and brown water affects the optical properties of the water differently, the mechanisms by which they affect aquatic predators are also likely to differ. Therefore, this thesis aims at describing both the differences and similarities in effects of turbid and brown water on visual predators, and when during the predator´s lifecycle the effects are the strongest.

The specific aims for the included papers are (Paper I) to evaluate pigmentation-based prey selectivity in juvenile piscivores, foraging on plankton during early life stages. In the second paper (Paper II) I aim at describing where during the early life of a planktivore and a piscivore the effects of visual degradation are present and what prey types and sizes that are affected. Effects during early life may affect transitions between different prey types or sizes with consequences for fish growth and recruitment to larger size classes. The effects on adult stages of visual piscivores are evaluated in the next paper (Paper III) where prey-size selectivity is evaluated along with an analysis of which foraging-cycle components that may be affected by changes in visual conditions. Finally, the last paper (Paper IV) aims at determining the difference in importance between prey density and visual conditions for the growth of piscivorous fish. It describes the effects in a natural system where a whole lake has been manipulated for years by removal of planktivorous fish, leading to less turbid conditions. Through most papers (Papers I, II and III) there are comparisons between the different visually degrading agents, but paper IV only includes effects of turbidity.

METHODS

Study organisms

In all papers, except paper IV, pike (*Esox lucius*) have been used as a visual piscivore and roach (*Rutilus rutilus*) as a planktivores and as prey for pike. Pike and roach are two of the most common fish species in temperate Europe. In the last paper (Paper IV), individual growth rate of the equally common piscivore perch (*Perca fluviatilis*) was evaluated. As these species are widespread and occurs in high densities, it is likely that effects of changes in the optical environment affecting their foraging success may also affect the rest of the ecosystem through complex trophic interactions.

Quantification of visual conditions

Generally, turbidity and brown colouration by humic substances are measured in different ways, and as the mechanisms behind visual degradation differ, there is no single "best" method that can be used to measure the visual conditions in a standardised way. The traditional, "old-school", measure of visual conditions in lakes is the Secchi depth which is measured by lowering a white disk into the water.When it disappears from sight you slowly rise it again until it is just visible; this depth is the Secchi depth. This is a very simple and cheap method for quantifying the visual conditions and it is similar to the more high tech measurement of the attenuation coefficient, a measure of how much light is removed through scattering and attenuation per unit depth. Both these measurements include all different types of visually degrading agents, regardless if they scatter or absorb light. However, there are other measurements that are used extensively that are appropriate for each specific mechanism. Turbidity is measured in several different turbidity units (JTU Jackson Turbidity Unit, NTU Nephelometric Turbidity Unit or FTU or FNU Formazin Turbidity Unit or Formazine Nephelometric Unit) that are measured in similar ways. The most common way to measure turbidity is to send light into a water sample and measure how much light is scattered to the side. If more light is scattered, the sensor on the side registers a higher light intensity, meaning that there are more particles in the water that scatters the light. This is not an optimal way to measure humic water as the main mechanism for visual degradation in humic water is absorption. Humic water produce a very low turbidity measure as not much light reach the sensor, both because light is not scattered but also because it is absorbed. Therefore brown water and turbid water could be regarded as extremely different if only a measure of turbidity was used, even if the Secchi depth was similar. Coloured water is instead measured using transparent sheets of brown coloured plastics that are calibrated to a certain concentration of platinum in the water (mg Pt/L), or by the more modern measure of absorbance. Absorbance is measured in a similar way to turbidity but here the light hits the sensor directly after passing the water sample and the amount of light removed by the water is measured. The different measurements and the different mechanisms behind visual degradation in these substances results in problems when standardising the visual conditions for comparison.

The most important measure when attempting to standardise the visual conditions in experiments is not the turbidity or absorbance, but the actual distance a predator can see. Determining the distance that a predator can see in specific waters also relates to the search efficiency of the predator. Further, the Secchi depth has been shown to be a very good measure of visual conditions with regards to repeatability and low variability between observers (Steel & Neuhausser 2002). This may be partly due to that the measure integrates the visual conditions in a large volume of water (everything between the observer and the disk) compared to measuring turbidity and absorbance in a few mL of a water sample. Small sample volumes increase the variance as the visual conditions depend on both depth and location where the sample is taken. Also, as contrast is extremely important for the detection of objects in the water we have combined the Secchi approach with contrast detection. In detail, as the observer looks through the wall of the aquaria, a vertically held disk with two black and two white fields is moved away from the observer. The visual range is defined as the distance where the difference between the white and the black fields of the disk is no longer distinguishable, i.e. where the contrast between the fields disappeared. This is, in my opinion, a very sound measurement of the visual conditions experienced by the fish. However, it does not take into account that light levels drop with the depth differently in different media, which is why all experiments were performed in shallow water to ensure that light levels were comparably high throughout the water column in all treatments. Also, the method assumes that fish vision is comparable to human vision which is indicated to be the fact for pike (Ranåker, L., Jönsson, M., Nilsson, P. A. & Brönmark, C. unpublished data).

Experimental setup

Several different experimental setups were used with different sizes and shapes which are dealt with in detail in the different papers (Paper I, II and III). However, there are some common methods that are important for the repeatability of the experiments. As mentioned before, the visual conditions are very important for the comparisons and standardization between the different visually degrading agents (se "Quantification of visual conditions" above). As several fish species are known to be able to utilise both the part of the light spectra that is regarded as the visual part for humans and the UV part, it is important that all wavelengths that are naturally present in sunlight is also present in our laboratory setups. For this reason, halogen spotlights have been used as they have a broad spectra of wavelengths ranging from UV to infra-red wavelengths. They have rather low intensities in the UV part of the spectra but is much better, with regard to wavelengths distribution, than for instance fluorescent light which have a few very intense peaks at certain wavelengths. Also, halogen light have rather high intensities in the wavelengths where pike (λ max: ca 525 nm) and roach (λ max: ca 530 nm) have their maximum visual sensitivity (Jokela-Määttä et al. 2007). Light from the halogen spotlights have in all experiments been reflected back into experimental arenas or have passed a diffusing white fabric to remove shadows and create as even light conditions as possible throughout the experimental arenas.

Field survey

The field survey was conducted in biomanipulated Lake Finjasjön, Sweden. The lake was eutrophied by sewage water and diffuse nutrient run-off from the surrounding land which resulted in severe algal blooms rendering the water inappropriate for swimming and drinking. Since 1990 there have been several attempts to restore the lake through biomanipulation (manipulation of the organisms to induce trophic cascades). The biomanipulations have been rather successful, which is often measured as the change in Secchi depth (see "Quantification of visual conditions"). Before the biomanipulations started, the Secchi depth was 0.35 meter but increased to 1.16 meter in recent years. This improvement in visual conditions is due to a trophic cascade, induced by the removal of a large part of the planktivorous fish guild. By removing zooplanktivores, zooplankton were released from their former predation pressure and allowed to increase in density. The many zooplankton exerted a much higher grazing pressure on phytoplankton than before which results in lower phytoplankton biomass. As phytoplankton was the main cause of visual degradation in the lake, the water clarity increased. However, what I am interested in is how the larger piscivorous fish are affected. On the one hand, the visual conditions improved, which should be positive for a predator that depends on vision for prey detection. On the other hand, about 80% of the prey fish that these predators feed on was removed during the manipulations. This lake therefore provides a unique opportunity to test the effects of visual conditions versus prey density on predatory fish *in situ*.

To evaluate the foraging success of the predatory fish, I estimated their individual growth rates. Growth analysis of perch were performed by the County Board of Skåne before the start of the biomanipulation project in 1990 and I repeated the procedure in 2008. The opercular bones were used for growth analysis (Le Cren 1947) with supporting age analysis of otoliths (Kleiven & Linlokken 2009). Both have a ring-shaped structure where more calcified white rings are formed during fast growth in spring and summer, and more transparent rings are formed at low growth rates during winter. The opercular bone is located in the gill operculum and grows in proportion to the body length of perch (paper IV), which makes it possible to back calculate the size of each fish at any given age (Figure 4). To do this you locate the start of the white high-growth rings which corresponds to the onset of spring growth after winter. Using the size of the bone at that ring allows you to back calculate the size of the fish at that specific time. The otoliths on the other hand do not grow in proportion to the body, but they give a more reliable age estimate. They are the counterparts of our hearing bones in our inner ear and they are located in the head of the fish. They are used for acoustics and balance, just as ours. By combining the two methods, both age and growth determinations produce more reliable results.

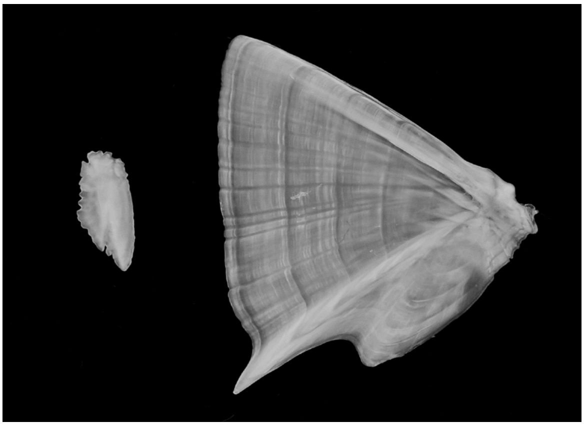

Figure 4. Otolith and opercular bone from perch used for age and growth analysis. Yearly growth rings are visible on the opercular but the otolith needs to be buned and broken i half to show growth rings.

SUMMARY AND DISCUSSION

Visual foraging in YOY fish

Most fish species hatch in early spring and are typically in the size range of 10-15 mm long. When hatching they still have part of their yolk sack left which provides nourishment during the first days of their life (Raat 1988). Thereafter, they have to start feeding to be able to maintain high grow rates which are of crucial importance for their survival (Chick & Van den Avyle 2000). Competition may be severe as there are enormous amounts of hatchlings and it is not many of them that survive. It is therefore crucial that they grow fast so they can compete for food and thereby continue to maintain high growth rates. As they are rather small they cannot consume very large prey, which is why most fish, regardless if they become large piscivorous predators or if they are small planktivores throughout their lives, feed on small zooplankton during their first weeks after hatching. Fish are gape-size limited predators and as they grow larger, their mouth also grows and they are continuously able to consume larger and larger prey (Mittelbach & Persson 1998). Larger prey are more energetically favourable as a consumer has to spend more energy to catch a larger number of small prey in order to consume the same amount of food (Post 2003). When an individual reaches a size, which allows it to switch to a larger, more desirable, food source it goes through an ontogenetic diet switch. These switches are crucial for maintaining high growth rates as the fish grows larger (Post 2003). The European perch is a well known example of a species that goes through ontogenetic diet shifts with a planktivorous, benthivorous and piscivorous phase (Persson 1983; Mittelbach & Persson 1998). However, species such as roach and pike also goes through diet switches. During their first days of life, pike are only able to feed on small copepods, rotifers and juvenile stages of other zooplankton, but after a while they can start to consume larger *Daphnia*. In comparison to perch, pike have a very short planktivorous stage as they may start to feed on other fish, including smaller pike, already at a size of around 30 mm total length which was seen during preparation for the experiments in paper II.

Visual foraging theory predicts that predators feeding on small prey detect their prey from very short distances. Reaction distance can be as short as 2-3 cm (paper II). However, several studies have reported that reaction distance to plankton prey increases in waters with low turbidity (Boehlert & Morgan 1985; Gregory & Northcote 1993; Utne 1997). This has been suggested to be due to that back scattering of light in turbid water behind the prey provides a very bright background. This backscattering increases the contrast between the prey and the background and thereby increases the reaction distance. At higher levels of turbidity the amount of particles between the prey and the predator outweigh the positive effect of backscattering and the effect of higher turbidity is therefore negative on the reaction distance. However, in paper II, I show that juvenile pike in water with low humic substance concentrations also experience increased reaction distance, even if backscattering is at a minimum (Figure 5), implying that another mechanism must be functioning in humic water. This increase in reaction distance did not result in changes in consumption, moving pattern, activity or foraging effort in pike. Further, there were no effects whatsoever of visual conditions on juvenile roach foraging on both small copepods and larger *Daphnia* (Paper II). It is therefore unlikely that the increase in reaction distance to small prey is of ecological relevance as the concentrations of zooplankton in early spring in habitats occupied by newly hatched fish, vegetation borders and shallow littoral habitats, may be extremely high.

Even if foraging efficiency as a whole is not affected by the visual conditions when fish are foraging on zooplankton, prey selectivity may differ between turbid and humic water Going back to the importance of background contrast, it may not only be the difference in brightness that gives contrast but also differences in colour between the prey and the background. In an experiment with differently pigmented prey, calanoid copepods with different levels of red carotenoid pigmentation, prey selectivity of pike differed between algal turbid and humic water (Paper I). Pigmentation in freshwater copepods generally range from transparent to bright red as they are pigmented by carotenoids (Hairston 1979; Hessen & Sörensen 1990; Hylander et al. 2009). Generally the pigments function as protection from harmful UV-radiation but at the same time they make the copepods more conspicuous to fish predators, indicating that there is a UV-protection/predation threat trade-off (Hairston 1976; Luecke & Obrien 1981; Hansson & Hylander 2009). In lakes with high predation pressure on copepods from fish, the copepods reduce the level of pigmentation so they appear transparent and are therefore more difficult for a predatory fish to detect. However, even if UV-radiation is attenuated in the surface layers of humic lakes and UV-radiation therefore does not pose a large threat to the copepods, there is still pigments present in copepods if they are under predation from fish (Hylander et al. 2009). The red pigment function as camouflage against the dark brown background in humic water, decreasing both the attack rate and consumption by fish compared to transparent prey (Paper I). The same red pigmentation, on the other hand, increased the attack rate and consumption by the pike if they were swimming in algal turbid water. In the algal turbid water backscattering result in a brighter background and together with the difference in colour between the green background and the red prey, it makes the red copepods more conspicuous (Paper I). Humic water may therefore also increase contrast between the prey and the background similarly to turbid water but not by backscattering but by providing a background with a contrasting colour, which may be one reason for the increased reaction distance in pike foraging on *Daphnia* in humic water (Paper II).

When pike were fed young-of-the-year (YOY) roach, their reliance on visual detection from a greater distance was immediately apparent. At this developmental stage, turbidity and humic water severely diminished the reaction distance of pike to fish prey (Paper II) which is in consistence with earlier studies on reaction distance in piscivorous predators (Vogel & Beauchamp 1999; Mazur & Beauchamp 2003). As prey increase in size, so does the dependence on long distance detection (Vinyard & O'brien 1976; De Robertis et al. 2003). In my experiments, the reaction distance of pike in clear water was 24 cm, which may be regarded as the maximum visual ability of pike at that developmental stage and under the specific experimental conditions. At the same time, the visual range in the algal turbid and in the humic water was 25 cm, i.e. the visual range in the water was not reduced beyond the pike´s visual ability. However, the visual conditions was apparently deteriorated to such an extent that reaction distance of pike foraging on fish prey decreased to 13.6±5.1 cm (mean±SD) in turbid water and 8.7±2.7 cm in brown coloured water (Paper II). A reduced reaction distance severely limits the volume of water that can be searched per unit of time with effects on the encounter rate with prey and thereby also potentially prey consumption. However, there was no difference in consumption rate between any of the treatments indicating that pike were able to compensate for the reduced encounter rate.

Others have found that, under degraded visual conditions, fish may change their activity pattern (Jacobsen et al. 2004), and they become more actively searching for food in order to encounter more prey (Meager & Batty 2007) but in this experiment I found no difference in either the distance or time spent swimming by pike. They instead compensated the reduced encounter rates by increasing their foraging effort through increased attack rates which is in compliance with earlier studies on piek foragin in turbid water (Engström-Öst & Mattila 2008). This is also consistent with a marginally significant decrease in capture success in visually degraded water.

As everybody knows, there is always a bigger fish. If juvenile pike were to increase their activity to counteract the reductions in encounter rates caused by degraded visual conditions they would expose themselves to larger predators and there are many larger pike as well as other species that consider YOY fish a suitable prey. Engström-Öst & Mattila (2008) found that juvenile pike actually decreased their activity in turbid water, supporting this idea. Further, there are always individual differences in growth rates among YOY pike and cannibalism is therefore very common. By using attack rate to compensate for the reduced encounter rate, YOY pike may avoid the large increase in predation risk associated with a more actively swimming foraging strategy. This may be a specific response to high levels of cannibalism which characterize dense pike populations (Raat 1988).

For YOY fish the effects of turbid and brown coloured water are similar, but in nature, turbid lakes are very different from humic lakes. Lakes with high algal turbidity are characterised by high nutrient availability and primary productivity that transfers into high availability of food resources, also for higher consumers. High prey density may therefore buffer the negative effects of a reduced reaction distance. Humic lakes, on the other hand, are characterised by low light penetration, and low productivity with low food resources for consumers at higher trophic levels (Karlsson et al. 2009). Here, a reduced reaction distance will have severe effects on encounter rates as prey density is low. If the lower encounter rates are compensated by increased foraging effort, through increased attack rate, this may lead to an increase in energy expenditure during foraging. The benefit of switching prey type may therefore decrease, resulting in delayed diet switches and reduced growth. However, Estlander et al. (2012) found that the diet switch from plankton to benthic prey in perch occurred at smaller perch sizes in highly humic lakes. This may be due to difficulties finding the small plankton compared to more stationary benthic invertebrates and the earlier switch probably helps maintain high growth rates in perch. At present, there are no studies indicating how the switch from stationary benthic prey or zooplankton prey to highly mobile and evasive fish prey are affected by visual conditions.

Visual foraging in adult fish

As the fish grows and becomes part of the adult population, the size of its prey also increases and thereby there is a potential for larger effects of visual degradation. Diverse effects of turbid water have been reported in the literature, including reduced encounter rates (Turesson & Brönmark 2007), but also behavioural changes such as changed activity patterns (Jacobsen et al. 2004; Meager & Batty 2007; Engström-Öst & Mattila 2008), decreased predator avoidance behaviours

(Miner & Stein 1996; Jacobsen et al. 2004; Lehtiniemi, Engstrom-Ost & Viitasalo 2005; Engström-Öst & Mattila 2008) and collapsed prey selectivity (Abrahams & Kattenfeld 1997; Reid, Fox & Whillans 1999; Shoup & Wahl 2009). However, in contrast to fish feeding on plankton, there is no published study on effects of humic water on individual level patterns of foraging in piscivorous fish.

Prey size selectivity have been found to decrease with increasing turbidity (Abrahams & Kattenfeld 1997; Reid, Fox & Whillans 1999), which indicate an inability in piscivores to select the most preferred prey as the image quality decreased. This is in accordance with our results, where size selectivity of pike foraging on five different size classes of roach collapsed completely in turbid water (Paper III). If the absence of selectivity in turbid water is due to image degradation through scattering, then selectivity should be maintained in humic water where the effect of scattering is low. This was also the case, pike showed the same preference for small prey in brown coloured humic water as in clear water (Paper III). They are able to select small prey that should be more difficult to detect or detected from shorter distances compared to the larger size classes (Aksnes & Giske 1993). In both turbid water and humic water, the visual range was standardised to 1 meter. This is a clear indicator that turbid water has more severe effects on the experienced image quality than brown coloured humic water (Paper III). As scattering in turbid water changes the direction of the image forming light, the image is blurred and the assessment of how appropriate the prey is, is compromised. A blurry image may not only affect the identification of the prey to a certain species or size but it may also affect the assessment of swimming speed, direction and orientation. Pike consistently swallow prey head first (Raat 1988) and mistakes in assessing the position and speed of a prey may result in lowered precision in the attacks and thereby more handling before the prey can be swallowed. This is especially important when there are other pike present as pike is both cannibalistic and cleptoparasitic (Raat 1988) . Pike tends to select prey that minimises the handling time to avoid prolonged exposure to cannibalistic and cleptoparasitic conspecifics (Nilsson & Brönmark 2000). The loss of selection of small prey and an incorporation of larger prey in the diet may thus increase risk for pike through increased handling time.

Reduced attack precision should also reduce the capture success of the predator, but I found no effect on capture success in turbid water (Paper III) which is where image quality is worst. However, there was a non-linear effect on capture success in humic water. Capture success was high in both clear water and in high DOM, but low in low DOM (Figure 3e in paper III). The visual range in the brownest treatment was 0.5 meter, which corresponds rather well with the maximum attack distance of pike of the sizes used in the experiments. This means that pike may have been able to approach the roach prey and initiate an attack before roach detected the pike. This gives pike the upper hand and could be one reason for the extremely high capture success in the brownest treatment. However, as the effect is not present in turbid water, the unique optical properties of the humic water may disguise the pike while it is approaching its prey. As discussed in paper I, colour contrast may be important as the difference between the background and prey may differ both in brightness and in colour. In paper III, a dark green pike may be much better camouflaged in dark brown water than it is in bright grey clay turbid water, resulting in that pike may not be able to get close enough to initiate an attack before it is detected by its prey in turbid water. A similar effect is also reported by Meager et al. (2006) who estimated the escape probability of cod (*Gadus morhua*) exposed to a predator model to be highest in intermediate turbidity due to a poorly timed escape response. Further, the non-linear effect on capture success in humic water may depend on the attack distance of the predator, and thereby on predator size, which indicates that the effects of visual degradation on fish is size dependent. This potentially predator size dependent effect on capture success adds complexity to an already complex system, i.e. some sizes of predators may be favoured as the water is getting browner while others are disfavoured. This size dependent asymmetry in the effects of visual degradation may also change over time as the visual conditions change through continued brownification (Graneli 2012).

The reduction in visual range in both turbid and brown coloured water resulted in a decrease in encounter rate with prey (Paper III), which is in accordance with earlier studies (Turesson & Brönmark 2007). The reduced encounter rate is consistent in both turbid and humic water which is expected as the visual range is standardized to the same levels. However, pike did not counteract this decrease in encounter rate by increasing its prey searching activity. In turbid water there was no effect on activity, but in humic water, activity decreased with increasing DOM concentration, which is the opposite to the expected result (Paper III). As the water gets browner the light intensities decrease, possibly inducing navigational problems which may decrease the activity of the fish. This is supported by Mazur and Beauchamp (2003) who found that lake char (*Salvelinus namaycush*) tend to reduce their activity at low light intensities. The reduced activity in pike in humic water is most likely linked to low light intensities as the same effect is not present in turbid water.

It is difficult to translate the individual effects from our highly controlled, small scale experiment to real life effects on fish in natural lakes. An alternative may be to perform whole-lake experiments where conditions are less controlled than in experimental settings, but the result may be more naturally relevant as the conditions are more natural. Whole lake manipulations for purely scientific purposes are not common, but lakes that have been subjected to eutrophication, which results in turbid conditions, are sometimes restored by biomanipulations (see "field survey" part of the Methods chapter). This may provide an opportunity to test the effects of changes in turbidity on piscivores in natural systems. However, in a natural lake it is difficult to evaluate separate foraging cycle components as it is not possible to follow single individuals to evaluate encounter rates, capture success, activity etc. On the other hand, it is possible to measure parameters that are consequences of all the above actions, e.g. individual growth rate. In paper IV the individual growth rates of the visual piscivore perch is evaluated before and after biomanipulation of Lake Finjasjön, Southern Sweden.

Individual growth rate incorporates all foraging components into a single measurable variable that can be used as a measure of foraging success. It is basically the intake rate, how efficiently the food is converted into growth and how much of the energy that is used for other activities. Before the biomanipulations started in 1990 the County Board of Skåne performed age analysis of many different fish species, including perch. At that time the Secchi depth in the lake was 0.35 meter and around 2008 when we sampled the lake again and analysed perch growth rate, the Secchi depth had increased to 1.16 meter. During these years the lake was also part of a survey fishing program that consists of one fishing event per year where nets with multiple mesh sizes that non-selectively catch fish from around 5 cm total length and larger were used (Appelberg 2000). The data from these survey fishing events can be used to evaluate how the fish assembly changes between years. The goal of the biomanipulations was to remove 80 % of the planktivorous biomass to release the zooplankton from predation and allow them to increase in number, and hence increase their grazing pressure on phytoplankton, resulting in reduced turbidity. Survey fishing data shows that both relative biomass and density of potential prey for piscivorous perch decreased 10-fold after the biomanipulation and this reduction in prey availability should have severe effects on perch growth rates. However, even though prey density decreases severely, perch were still able to grow faster after the biomanipulation, probably due to the improved visual conditions that increase the search efficiency of perch (Paper IV). Hence, the visual conditions are more important for a visual piscivore than prey density which is in accordance with Turesson and Brönmark (2007) who found that encounter rate is more dependent on visual conditions than prey density in lakes of different trophic status.

GENERAL CONCLUSIONS

Visual conditions are changing in several different ways. Some lakes are getting turbid due to eutrophication or erosion while others are getting browner due to brownification. These two types of visual degradation results in completely different optical properties of lakes. Turbid water scatter light which degrades image quality severely while brown coloured humic water mainly absorb light making the aquatic environment darker.

In juvenile fish, the effects seem to be similar between turbid and humic water where foraging of planktivorous life stages are largely unaffected. However, prey selectivity in juvenile fish may change as red carotenoid pigmentation in copepod zooplankton make them more conspicuous in turbid water while transparent copepods are selected by the fish in humic water. The pigments, that are usually used for UV-protection in clear water, may therefore make the pigmented copepod cryptic in humic water, explaining the presence of the pigments in brown waters where UV-radiation is very low.

Piscivorous juvenile fish experience negative effects of visual degradation, including reduced reaction distance which reduces the search efficiency and encounter rate for the predator. Juvenile pike are able to counteract the reduced encounter rate with increased attack rate and thereby probably also higher foraging effort. This increase in foraging effort when foraging on fish prey may reduce the benefit of ontogenetic diet switches and thereby have consequences for growth and recruitment in fish populations.

Foraging in adult fish depend heavily on visual conditions. For adult fish, image quality is important, resulting in that prey size selectivity collapses completely in turbid water. In clear water pike consistently selects small prey to reduce handling time to a minimum. This selectivity for small prey are maintained in brown humic water. Lost selectivity in turbid water and thereby capture of larger prey than necessary, increases the handling time of prey, and thereby the exposure of pike to cannibalistic and cleptoparasitic conspecifics. However, the most pronounced foraging cycle effect of visual degradation is the reduced reaction distance that lowers the search efficiency of the predator and thereby possibly the encounter rate with prey. Decreased encounter rates was however not counteracted by increased search activity. The importance of the visual conditions for the encounter rate is also implied when growth rate of perch was evaluated before and after biomanioulation of Lake Finjasjön. A 10-fold decrease in relative prey biomass and density after biomanipulation is completely counteracted by improved visual conditions where Secchi depth increased from 0.35 m before to 1.16 m after biomanipulaton. This resulted in increased growth in the predator, probably due to increased encounter rate, despite the 10-fold decrease in prey density.

FUTURE PERSPECTIVES

There are two major areas that I find especially interesting to develop further regarding visual foraging in fish. The first is how fish adapt to these conditions and thereby counteract the effects of visual degradation. The other is how visual conditions degrade the experienced image quality of the predator.

Visual adaptation

Fish are usually regarded as very plastic, meaning that they change during their lifetime to be better synchronized with the demands of their environment. This is in contrast to evolutionary changes that result in a change in gene composition through natural selection. Fish living in dark environments may have several adaptations that help them cope with unfavourable visual conditions. One factor that is often discussed is eye size. Does a larger eye allow for better vision? Is development of eye size plastic? Is eye size a result of local adaption to prevailing environmental conditions, i.e. a genetically fixed trait? Preliminary unpublished data on eye size in perch suggest that eyes are larger in both turbid and brown coloured lakes regardless of resource levels. Others have suggested that large eyes in turbid water is a result of poor nutritional status and not an adaptation, but this is contradicted by our preliminary data. As perch is a very plastic species that change morphology in response to environmental factors (Svanbäck & Eklöv 2006), adaptation in the eyes may also occur in visually degraded environments. Other parameters may also change due to restricted visual conditions like the lens size, retinal structure etc. We also have indications that the visual conditions affect cornea colouration, which adds a colour filter in front of the lens that removes certain wavelengths. If this is a passive process where the wavelengths that are not used are filtered away because there is no selection for keeping them or if it is an active process where the removal of these wavelengths in some way improve the visual performance of the fish is unknown.

Quantification of image quality

From the previous part of the thesis it is hard to avoid to see that I am very interested in image quality. Image forming light is reflected on particles on its way between the object and the detecting eye. Resolution and contrast detection can be measured for fish in experimental setups. However, I am not interested in the absolute resolution of a specific fish eye but more the change in perceived resolution or the change in contrast detection when individual fish are subjected to different environmental conditions. This also adds a possibility to evaluate the potential differences on pre-exposure to degraded visual conditions by using fish from environments with different visual conditions. Adaptations that optimise performance in humic or turbid water will most likely not be optimal under clear water conditions. The naturally following question would then be if this adaptation is plastic and changes over an individual's lifetime or if it is genetically coded and remains even if the visual condition change over time. Most likely it is a combination of the two but the relative importance of them is very important for the ability of individuals to deal with changing visual conditions trough the effects of continued climate change.

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Acknowledgement

I will write this extended thanks in Swedish as most people that are included, speak or understand Swedish.

Först, **Ullis**, som gett mig tid att slutföra mitt arbete men även upptagit min tid i de fall då jag inte själv klarat prioriteringarna, och för att ha gett mig det bästa av alla världar. Till **Alva** och **Nora**, de två ständiga ljusen som tillför livet allt från mening till obegränsad glädje och frustration. Dessutom är det ju tacksamt att förskolepersonalen tror att jag jobbar i en akvarieaffär, kan knappt vänta tills Nora ska försöka förklara det...

Till **handledarna**, eller som jag kallar dem “de med den röda rollern”. Utan rollern hade jag skrivit betydligt sämre än vad jag gör idag, trots att den inte är så omtyckt. **Christer** har varit en inspirationskälla som delat med sig av ett spännande ämne och gett mig ganska lösa tyglar att arbeta under, vilket utvecklat min självständighet. **Anders** är bra då intresset för ämnet tryter, uppmuntrande och allvarssam när det behövs, men kanske framför att för insikten i att man alltid kan söka tröst i några statistiska transformationer eller djupt inne i en multivariat statistik när resultaten inte går ens väg.

Till mina **föräldrar** som alltid stöttat mina beslut och uppmuntrat till livsval som kanske inte alltid varit de smartaste men troligtvis de som gett mig mest behållning och dessutom de som är mina egna. Till min **syster** för att jag alltid har haft någon att tävla mot, trots att det är omöjligt att vinna. Jag van dock den ultimata tävlingen med 83 dagar, det kan jag leva på ett tag ;)

Till **Lynn** för givande diskussioner och samarbete trots att våra handledare inte trott att vi pratade med varandra. Dessutom för mycket trevliga fältturer, trots vissa inducerade sömnproblem och brist på kunskap i hur man sätter upp tält... Till **Peter** som numera är min semi-sambo för upplyftande bitterhet och djupa diskussioner som bara två plågade själar kan framkalla och som är den naturliga följden av att dela en flaska Fernet. **Kullberg** för att jag uppskattar *Scenedsesmus*-shot och ditt festsinne betydligt mer än din datorsupport. **Ronald** för att det

senaste året gett mig ny inspiration när den gamla började tryta och för ett mycket intressant och givande samarbete, även om det innebar långa fiskedagar då jag istället borde skrivit på avhandlingen. **Mikael** för åldersanalys och försök som gick åt pipan, nu slapp jag slösa bort min egen tid. Dessutom tack för all hjälp när jag kört försök och varit tvungen att hämta på förskolan och liknande. And **Melanie**, thanks for appreciating the slightly morbid comments that come out of my mouth without my knowledge, I thought I was the only one. Och sist i detta stycket, **Leo** även om whiskeyn var god så är det nog dags att du hittar en ny leverantör av bättre begagnad fisk...

Tack till **Barilochegänget** för en fantastisk resa, vinet, köttet, ölen, carcason och Fernet, kan det bli bättre. Dessutom tack till alla **medförfattare** för fantastiskt sammarbete och till **frukustklubben** för den paus det innebar att få äta sin "second breakfast" och hela **Akvatisk ekologi** för att ni gör det till ett nöje att komma till jobb, även om man får mest gjort hemma på slutet. Till alla andra som hjälpt mig på labb eller i fält och de som täckt upp för mig när jag hämtat på förskolan, vabbat eller själv varit sjuk.

Till alla vänner och bekanta som stöttat och frågande undrat vad det igentligen är jag håller på med, är jag nu tillräcklig förberedd för att svara: **"Jag har slutat!"**

My contribution to the papers

I. Foraging success of juvenile pike Esox lucius depends on visual conditions and prey pigmentation

I had the original idea which was further developed together with Samuel Hylander. I did the experimental setup and performed the experiments together with Samuel Hylander. I analyzed the data and wrote the paper with contributions from Samuel Hylander and Lynn Ranåker, Anders Nilsson and Christer Brönmark.

II. Prey-type dependent foraging success of young-of-the-year fish in turbid and humic environments

From the original idea by Christer Brönmark, I designed the experiment together with Lynn Ranåker, Anders Nilsson and Christer Brönmark. I performed the experiments together with Lynn Ranåker and analyzed the data with contributions from Anders Nilsson. I wrote the paper with contributions from Christer Brönmark, Anders Nilsson and Lynn Ranåker.

III. Prey selectivity and foraging behaviour in pike (Esox lucius): effects of turbid and humic water

From the original idea by Christer Brönmark, I designed the experiment together with Anders Nilsson and Christer Brönmark. I performed the experiments with contributions from Jens Persson and Peter Johannessen and analyzed the data with contributions from Anders Nilsson. I wrote the paper with contributions from Christer Brönmark, Anders Nilsson and Lynn Ranåker.

IV. Clear-water conditions increase perch (Perca fluviatilis) growth regardless of prey density in a biomanipulated lake

From the original idea by Christer Brönmark, I designed and executed the field sampling and Mikael Ekvall performed the age analysis with assistance from me. I analyzed the data together with Mikael Ekvall with contributions from Anders Nilsson. I wrote the paper with contributions from Mikael Ekvall, Christer Brönmark, Anders Nilsson and Lynn Ranåker.

I

Foraging success of juvenile pike *Esox lucius* depends on visual conditions and prey pigmentation

Journal of Fish Biology (2011) **79**, 290–297
doi:10.1111/j.1095-8649.2011.03004.x, available online at wileyonlinelibrary.com

BRIEF COMMUNICATIONS

Foraging success of juvenile pike *Esox lucius* depends on visual conditions and prey pigmentation

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(Received 24 August 2010, Accepted 12 April 2011)

Young-of-the-year pike *Esox lucius* foraging on copepods experienced different foraging success depending on prey pigmentation in water visually degraded by brown colouration or algae. Both attack rate and prey consumption rate were higher for *E. lucius* foraging on transparent prey in brown water, whereas the opposite was true in algal turbid water. Pigments in copepod prey may have a cryptic function in brown water instead of a photo-protective function even if prey-size selectivity was stronger than selection based on pigmentation in juvenile *E. lucius*.

Key words: background contrast; cryptic pigmentation; turbidity; vision; water colour.

Most fishes undergo ontogenetic diet shifts during early development (Crowder & Crawford, 1984; Luecke, 1986). When hatching they are severely gape size limited. During growth, gape size and prey-size 'windows' increase, and shifts to larger prey items are possible (Wong & Ward, 1972; Werner, 1974; Unger & Lewis, 1983). These ontogenetic diet shifts also change predation pressures across prey communities and thereby incur consequences for trophic interactions. Most fish species have a planktivorous early life stage, even piscivorous fishes such as pike *Esox lucius* L. 1758 (Raat, 1988). The ecological consequences of planktivory from such fishes have received comparably little attention even though success at the planktivorous stage governs growth into piscivory. Optimal timing of the transition to piscivory is of fundamental importance for individual growth and recruitment to larger size classes and thereby also for predation rates and recruitment of young-of-the-year (YOY) prey fishes.

Copepods constitute an abundant food source for YOY fishes. The copepods adjust their pigmentation in response to a UV protection and predation risk trade-off (Hairston, 1976; Luecke & Obrien, 1981; Hansson, 2004; Hansson & Hylander, 2009). In brown water lakes, with high UV attenuation (Davies-Colley & Vant,

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1987; Kirk, 1994; Morris *et al*., 1995), the photo-protective benefit of the pigment should be reduced but pigmentation does not decrease with increasing brown colouration in lakes with medium to high fish predation pressure (Hylander *et al*., 2009*a*). Accumulation of pigments is costly, as indicated by reduced pigment levels in copepods when released from UV radiation (Hylander *et al*., 2009*a*, *b*), suggesting that other factors maintain pigmentation levels in brown water. Background illumination is important for prey detection as it increases the contrast between background and prey (Utne-Palm, 1999*a*). Turbid water provides a bright background because of backscattering of light while brown coloured water instead provides a dark background where light is absorbed instead of backscattered. With a dark background, red pigments may have a cryptic instead of a UV-protective function. Changes in visual conditions may therefore affect the costs and benefits in the photo-protective and predation avoidance trade-off in copepods, ultimately affecting prey pigmentation and the selectivity and foraging success of fish feeding on them.

Temporal changes in water clarity are common, including brown colouration during recent decades (Hongve *et al*., 2003; Monteith *et al*., 2007; Erlandsson *et al*., 2008) and algal blooms making the water more turbid (Anderson *et al*., 2002). Therefore, the effect of visual conditions, brown coloured or algal turbid water, on foraging in YOY *E. lucius* was evaluated with two levels of prey pigmentation. Copepods are a suitable model prey as juvenile *E. lucius* prefer large copepods and cladocerans (Raat, 1988; Salonen *et al*., 2009). *Esox lucius* foraging efficiency on transparent copepods is hypothesized to be higher than for pigmented copepods in brown water while the opposite is expected in algal turbid water. In addition, given a choice, YOY *E. lucius* are expected to positively select for transparent copepods in brown water and pigmented copepods in algal turbid water.

Esox lucius (2 weeks old, hatched at 15° C) were collected from a Swedish hatchery (Lake Bäsingen, 60° 09′ N; 16° 20′ E) where they had been continuously supplied with lake water containing the zooplankton present in the lake at that time. They were transported to the Aquatic Ecology section, Lund University, Sweden, where they were kept in 70 l flow-through holding tanks (*c*. 200 *E. lucius* per holding tank) at 18° C in fluorescent light (GE Lighting Polylux XLR, 85Wx2, General Electric Company; www.gelighting.com) with 14L:10D cycles. They were fed in excess once a day with a natural zooplankton community, following a succession from rotifers in spring to a dominance of copepods during early summer, from a nearby pond until reaching a suitable size for copepod foraging experiments [*E. lucius*, 4 weeks old, total length (L_T) 18·5 ± 1·0 mm, mean ± S.D.].

Pigmented calanoid copepods were collected in a clear-water system with low fish densities (Dalby Quarry, 55° 39′ N; 13° 24′ E) and the transparent calanoid copepods from a eutrophic lake with high fish biomass (Lake Häljasjön, 55° 40′ N; 13° 32′ E). The dominant copepod species in the samples was *Eudiaptomus gracilis*. Freshwater copepods generally display a distinct red colouration (Hairston, 1979; Hessen & Sörensen, 1990; Hylander *et al*., 2009*a*) with an absorption peak at 474–478 nm, indicative for the carotenoid astaxanthin (Hairston, 1979; Britton, 1985). A few reports on blue or green copepods with protein-bound carotenoids exists (Luecke & Obrien, 1981) but no such morphs were observed among the copepods. Other pigments, apart from carotenoids, have generally not been found in extracts from freshwater copepods (Hairston, 1979; Hessen & Sörensen, 1990; Hylander *et al.*, 2009*a*). Samples for carotenoid analysis, containing 30–40 calanoid copepods each, were extracted in ethanol (95%) and analysed according to standard methods (Hylander *et al.*, 2009*b*). Quantification of the red pigment in the supernatant was performed with a Beckman DU 800 spectrophotometer (Beckman Coulter, Inc.; www.beckmancoulter.com) at 474 nm (Hansson, 2004; Hylander *et al.*, 2009*a*) and normalized to dry mass using length to dry mass relationships for calanoid copepods (Bottrell *et al.*, 1976). There was a clear visual difference between the copepod populations with one being almost transparent (carotenoid level: 1·9 ± 0·3 μg mg^{-1} dry mass, length: 1·1 ± 0·1 mm, mean ± S.D.) and one being distinctly red (carotenoid level: 3·0 ± 0·2 μg mg^{-1} dry mass, length: 1·1 ± 0·1 mm). Foraging efficiency and selectivity experiments were performed in square arenas (154 × 180 mm, 60 mm water depth) illuminated by two halogen lamps (R7s, 150 W) through a white fabric to create even and diffuse light conditions at 116 lx at the water surface and 76 and 45 lx at the bottom in algal turbid and brown coloured water, respectively (INS DX-100 Digital lux meter, INS Enterprise Co. Ltd; www.inss.com.tw). Photosynthetically active radiation (PAR) intensity was 2·45 μE m^{-2} s^{-1} at the surface and 1·42 and 0·93 μE m^{-2} s^{-1} at the bottom in algal turbid and brown coloured water, respectively, and UV radiation was 2·07 μW cm^{-2} at the surface and 1·45 and 1·24 μW cm^{-2} at the bottom in algal turbid and brown coloured water, respectively (NIST Traceable radiometer and photometer, International Light IL1400A with both PAR and UV sensor; www.intl-lighttech.com). A halogen light was used to ensure a broad spectrum of light (λ: 410–930 nm) that included the absorption peak in the eyes of *E. lucius* [λ: *c*. 525 nm (Jokela-Määttä *et al.*, 2007)] and most wavelengths were present at the bottom in all treatments due to the shallow depth (λ: 420–930 nm in algal turbid water and 460–930 nm in brown water, Ocean Optics HR4000 High-Resolution Spectrometer; www.oceanoptics.com).

Visual condition (algal turbid and brown coloured water) and prey pigmentation (transparent and pigmented copepods) were combined in a full factorial design with a total of seven replicates for each treatment combination, except for brown coloured water and transparent copepods which had eight replicates. Algal turbid water was prepared using a mixture of common green algae grown in the laboratory while brown water was collected from a nearby pond (Black pond, Frihult, 55° 33′ N; 13° 39′ E). The visual range in the water was defined as the horizontal distance between the human eye and a Secchi disc at which the contrast between the disc's black and white fields disappeared. This method of measuring visual range has been evaluated where reaction distance of *E. lucius* to fish prey corresponds tightly to the measured visual range (L. Ranåker, M. Jönsson, P. A. Nilsson, & C. Brönmark, unpubl. obs.). The turbid and brown water was diluted to the visual range of 0·25 m. A single 4 week-old *E. lucius* (L_T 18·6 ± 1·0 mm, mean ± S.D., $n = 42$) was acclimatized in each experimental arena for 30 min before the trial was started by introducing 40 copepods in the centre of the arena. The trial was terminated after 30 min by removing the *E. lucius*. The water was then filtered through a 50 μm plankton net and remaining copepods were counted. Water temperature was 21·1 ± 0·2° C (mean ± S.D.) during experiments. Trials were recorded from above and later analysed for attack rate (number of attacks), capture success (proportion of the attacks that resulted in ingestion) and consumption (number of zooplankton consumed). Each *E. lucius* was used only once and the effect of the treatments were analysed using MANOVA in IBM SPSS Statistics for Windows, version 19 (www.spss.com).

To evaluate selectivity, a single 5 week-old *E. lucius* (L_T 23·6 ± 1·6 mm, mean ± S.D., $n = 25$) was acclimatized in each experimental arena for 30 min before the trials were started by the addition of a copepod mixture (40 ml). The mixture was composed so that a third of the copepods were from the transparent population and two thirds from the pigmented population. This composition ensured that the mixture contained copepods with a large range of pigmentation and that changes in pigmentation should be detectable in both directions. Trials were terminated after 18 h and remaining copepods were collected. For each treatment, eight replicate trials were performed. Initial temperature was 20·7 ± 0·2° C (mean ± S.D.) and increased during trial time to 21·3 ± 0·4° C. From each trial and from four sub-samples of the initial mixture, copepods were randomly sampled for length (17–22 copepods per sample measured to the nearest 0·01 mm) and for carotenoid pigment analysis (30–40 copepods per sample). The mean value from the four sub-samples of the initial mixture constituted the start value in all trials. To comply with the assumptions of normality and homoscedasticity, changes in length and level of pigmentation were analysed on arcsin ($\sqrt{x}$)-transformed proportional change from mean start values. One sample t-tests were used in IBM SPSS Statistics for Windows, version 19.

There was no effect of either visual condition (Wilk's $\lambda = 0{\cdot}99$, $F_{3,23} = 0{\cdot}09$, $P > 0{\cdot}05$) or prey pigmentation (Wilk's $\lambda = 0{\cdot}80$, $F_{3,23} = 1{\cdot}88$, $P > 0{\cdot}05$) on juvenile *E. lucius* foraging. There was, however, an interaction effect between visual conditions and prey pigmentation (Wilk's $\lambda = 0{\cdot}70$, $F_{3,23} = 3{\cdot}36$, $P < 0{\cdot}05$). Univariate between-subject effects showed interaction effects on attack rate [$F_{1,25} = 5{\cdot}43$, $P < 0{\cdot}05$; Fig. 1(a)] and consumption [$F_{1,25} = 7{\cdot}21$, $P < 0{\cdot}05$; Fig. 1(c)] where both attack rate and consumption were higher for pigmented copepods in algal turbid water and for transparent copepods in brown coloured water. There was no interaction effect on capture success [$F_{1,25} = 0{\cdot}44$, $P > 0{\cdot}05$; Fig. 1(b)]. There was a significant reduction in mean copepod size during trials in both brown ($t = 8{\cdot}69$, d.f. $= 7$, $P < 0{\cdot}001$) and algal turbid water ($t = 5{\cdot}98$, d.f. $= 7$, $P < 0{\cdot}001$; Fig. 2). There was no change, however, in the level of pigmentation (carotenoid concentration) in brown ($t = 0{\cdot}92$, d.f. $= 7$, $P > 0{\cdot}05$) or algal turbid water ($t = 0{\cdot}59$, d.f. $= 7$, $P > 0{\cdot}05$; Fig. 2).

Different combinations of visual conditions and level of prey pigmentation had different effects on *E. lucius* foraging success. Carotenoid-pigmented copepods in algal turbid water produced a relative increase in *E. lucius* foraging, while pigmented prey in brown water reduced the foraging success (Fig. 1). This is probably due to background colour and brightness. Brown water, where a large part of the light is absorbed, provides a dark background where the detectability of pigmented copepods decreases. The pigments may therefore have a cryptic function in brown water where they are no longer needed for photo-protection due to the rapid attenuation of harmful UV radiation, providing a new mechanism to why levels of photo-protective pigments are maintained in waters with low UV threat and medium to high fish predation. The lack of decrease in the pigmentation level in brown water with medium to high fish predation supports the idea that pigmentation may reduce the risk of predation in brown water. In algal turbid water, where scattering of light is the main cause of visual degradation, scattering makes the background bright, making pigmented prey more conspicuous. As prey pigmentation in combination with visual conditions affects the foraging success of YOY *E. lucius*, it should also affect their growth. Early life growth is of fundamental importance for a number of reasons,

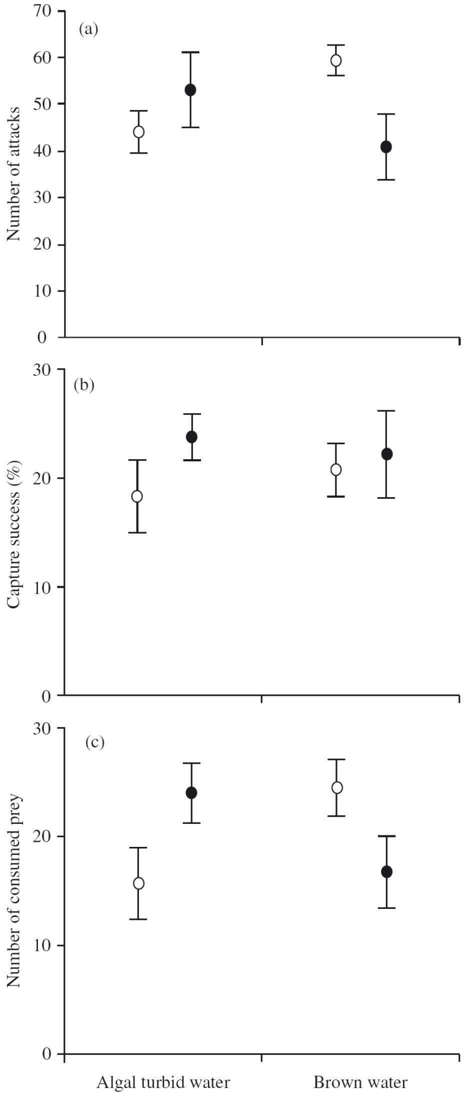

FIG. 1. Young-of-the-year *Esox lucius* (a) attack rate, (b) capture success and (c) consumption in two visual conditions (algal turbid water or brown coloured water) and on two levels of zooplankton prey pigmentation, transparent copepods (○) and carotenoid-pigmented copepods (●), in 30 min foraging trials ($n = 7$ for all treatments except in brown water with transparent copepod prey where $n = 8$). Values are means ± S.E.

for successful timing of the transition to piscivory and for decreasing the risk of size-structured cannibalism and predation (Bry *et al.*, 1995). By affecting foraging success, visually degraded environments expose *E. lucius* to different prerequisites for success during early life. The prey–background contrast should not only affect

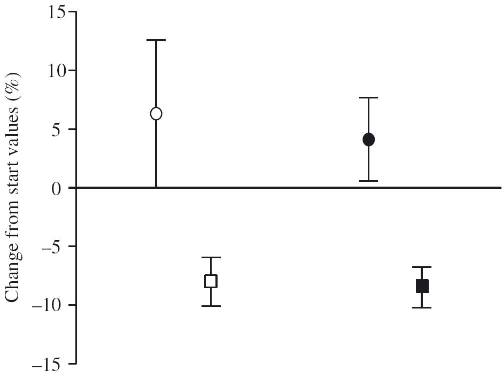

Fig. 2. Proportional difference (%) in copepod prey size (□, ■) and pigmentation (○, ●) between an added zooplankton assembly and the assembly after 18 h of young-of-the-year *Esox lucius* predation. Values show mean ± s.e. proportional difference in algal turbid (□, ○) and brown coloured water (■, ●) ($n = 8$ for all treatments).

larval *E. lucius* but any visually oriented planktivore (Utne-Palm, 1999*b*). The effect of brown water on planktivorous foraging should therefore be general among visually oriented fish species, with possible consequences for overall fish growth and recruitment. Both strict planktivores and generalist foragers should experience relatively reduced foraging and growth capacities with increased brown colouration of the water which is supported by lower fish catches in brown lakes than in other systems (Aksnes, 2007). Light limitation is proposed to be the major limiting factor for fish productivity in brown lakes (Ask *et al*., 2009; Karlsson *et al*., 2009) and fishes may therefore be restricted both by food shortage and impaired visual foraging efficiency. As the trend during the last decades strongly provides expectations for increased brown colouration in aquatic ecosystems in the future (Hongve *et al*., 2003; Monteith *et al*., 2007; Erlandsson *et al*., 2008), reductions in overall fish growth is anticipated in affected systems. In algal turbid systems on the other hand, food availability is often good resulting in less pronounced effects on individual growth and recruitment, making the brown water systems more sensitive to changes in transparency.

The relatively poorer foraging efficiency of *E. lucius* on pigmented copepods in brown water implies that *E. lucius* should increase selectivity for non-pigmented prey in brown water. As the present results did not show any relative changes in level of prey pigmentation, it is concluded that *E. lucius* larvae do not respond to this change in foraging efficiency. This result could be explained by *E. lucius* lacking the ability to distinguish between prey types, but as the results show clear size selection, inability to select prey is unlikely to be the cause. There is a possibility that prey density in combination with small arena size obscured the selection. It is fairly clear, however, that prey-size selectivity in larval *E. lucius* is more important than prey selection due to pigmentation level.

We thank J. Morén and the fishing preservation district of Lake Bäsingen, Sweden, for hatching and providing *E. lucius* larvae for the experiments and B. Chapman for constructive

comments. Experiments were approved by an ethical committee (Dnr M165-07) and facilities have permits for fish husbandry from the Swedish Board of Agriculture (Dnr 35-1878/03).

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II

Prey-type dependent foraging of young-of-the-year fish in turbid and humic environments

Ecology of Freshwater Fish 2012
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Prey-type-dependent foraging of young-of-the-year fish in turbid and humic environments

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Accepted for publication February 28, 2012

Abstract – Fish, which are generally visual foragers, experiences reduced reaction distance in visually degraded environments, which has consequences for encounter rates with prey. Small prey is detected at shorter distances than larger prey, and piscivores are therefore predicted to be more strongly affected by visual degradation. In experiments, roach (*Rutilus rutilus*) were fed two plankton prey types and pike (*Esox lucius*) were fed *Daphnia* and larval roach, in clear water, algal turbid water and water coloured brown by dissolved organic matter (DOM). Planktivorous foraging in roach was not affected by visual degradation, while pike foraging on both *Daphnia* and larval roach was. Pike showed increased reaction distance to *Daphnia* in visually degraded water, while it was severely reduced with roach as prey even if the visual range was not reduced below pike reaction distances in clear water. Pike foraging on *Daphnia* was not affected, but when foraging on roach, the reduced search efficiency was counteracted by increased attack rates. However, there was no increase in movement and no difference between turbid and DOM treatments. Effects on piscivores will likely become more pronounced at later life stages as prey size and the reliance on long-distance detection increases at the same time as changing climatic conditions may further deteriorate the visual conditions in future.

Key words: turbidity; humic water; foraging; prey size; juvenile fish

Introduction

Growth rate of juveniles is one of the most fundamental factors affecting survival and recruitment in fish populations (Chick & Van den Avyle 2000; Post 2003), and it depends heavily on the availability of resources. However, resource-specific benefits may change over time as most fish are gape-size-limited foragers with ontogenetic shifts in prey-type preference (Werner & Gilliam 1984; Mittelbach & Persson 1998). At different developmental stages, fish feed on different types and sizes of prey according to prey-type availability, gape-size limitations (Mittelbach & Persson 1998) and energetic gain (Stephens & Krebs 1986). Fish, which are generally visual foragers (Guthrie & Muntz 1993), detects larger prey from greater distances than smaller prey (Chesney 1989; Vogel & Beauchamp 1999; De Robertis et al. 2003). Therefore, foraging on larger prey may be more affected by reduced visual conditions than smaller prey, which indicates that the effects of deteriorated visual conditions on foraging in juvenile fish may change during early ontogeny.

It is previously known that increased clay turbidity affect foraging in fish, which is acknowledged as a major environmental problem (Lind 2003). However, eutrophication also increases turbidity by stimulating phytoplankton growth which also degrades the visual conditions in the water (Shapiro et al. 1975; Søndergaard et al. 2007). During the last decades, many lakes on the Northern Hemisphere have also experienced increased brown coloration, resulting in the further deterioration of the visual environment (Hongve et al. 2004; Monteith et al. 2007; Erlandsson et al. 2008). However, the optical properties of brown-coloured water are completely different from those of turbid water. In turbid water, large particles, that is, clay particles, phytoplankton or suspended sediment, scatter incoming light and thereby reduce the contrast between the prey and its background (Utne-Palm 2002). The brown colour on the other hand originates from dissolved organic matter (DOM) that absorbs

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doi: 10.1111/j.1600-0633.2012.00565.x

light instead of scattering it and leads to reduced light intensities (Davies-Colley & Vant 1987; Morris et al. 1995), but contrast may be maintained if light levels are sufficient. As contrast is one of the most important parameters for prey detection in fish (Hinshaw 1985; Utne-Palm 1999), foraging may not be as severely affected by DOM as it is by turbidity. There are indications that individual growth rates (Horppila et al. 2010) and fish production (Karlsson et al. 2009) are affected by the level of DOM in the water. However, even though this lake type is very common in the boreal region, experimental data on the effects of water with DOM on foraging rates in fish are scarce, but there has been some recent advances (Laine 2001; Horppila et al. 2011; Estlander et al. 2012). Light level and prey size (Chesney 1989; De Robertis et al. 2003) also affect the detection of prey (Vinyard & O'brien 1976; Aksnes & Giske 1993), implying that visual conditions may affect foraging on different prey sizes differently. Foraging may be affected through decreased encounter rates (Turesson & Brönmark 2007), which can be counteracted by increased activity (Jacobsen et al. 2004; Meager & Batty 2007). But the outcome of a predator attack also depends on behavioural decisions and accuracy in interpreting the surroundings by both the predator and the prey, that is, their abilities to assess vulnerability and risk. By decreasing the visual information available, the precision in these assessments may be affected.

As most fish are gape-size-limited foragers, they feed on prey of increasingly larger sizes during their ontogeny. Larger prey are generally more energetically favourable (Olson 1996; Mittelbach & Persson 1998; Post 2003), and shifts in prey size preference and/or windows can therefore be crucial for continued juvenile growth (Mittelbach & Persson 1998; Persson & Brönmark 2002). Reduced growth may reduce the competitive ability of individuals (Persson & Brönmark 2002) and expose juveniles to predators for a longer period, reducing probability of survival and thereby lifetime fitness. Individual success during ontogeny is thereby of crucial importance to both individual growth and population recruitment processes.

In this study, we evaluate the effects of visual degradation on juvenile fish by comparing activity, swimming pattern, reaction distance and foraging efficiency of YOY fish in clear water, algal turbid water and water coloured brown by DOM when foraging on two differently sized prey types. Copepods and *Daphnia* were used as small and large zooplankton prey for roach, and *Daphnia* and YOY roach as small and large prey for pike. We hypothesised that foraging on plankton prey is not affected by visual degradation because of small prey sizes and thereby very short reaction distances. In contrast, we expect that foraging on fish prey should be negatively affected by visual degradation because of a dependence on long-distance prey detection (Chesney 1989; Aksnes & Giske 1993; De Robertis et al. 2003). Reaction distances for pike were hence expected to be negatively affected by visual degradation when foraging on fish prey. Further, water with DOM was not expected to affect foraging and behaviour as severely as turbid water.

Methods

In the experiments, juvenile roach and pike were fed with different prey types at two different periods during early ontogeny. Experiments were run in clear water, turbid water (green algae dominated by *Scenedesmus* spp.) and water coloured brown by DOM. These treatments are hereafter referred to as clear, turbid and DOM water treatments.

Roach eggs were collected in Björkaån stream (55°39′N, 13°38′E), Sweden, spring 2009 (water temperature, 11.6 °C), where roach migrate to spawn. Eggs are deposited in thick mats on the substrate of shallow fast-flowing stretches of the stream and can easily be collected by hand and put in aerated water. Eggs were transported to the laboratory at Lund University where they were kept in aerated stream water that was allowed to slowly increase in temperature to 16 °C. Roach larvae hatched during the following 3 days. Hatched larvae were moved to rearing tanks where they were fed cladoceran ephippia, live rotatoria and copepods once per day. After 5 weeks, larger cladocerans were also included in the food.

Pike came from a hatchery at Lake Bäsingen (60°09′N, 16°20′E), Sweden, where they were continuously fed zooplankton from the lake. They were collected and transported to the laboratory at Lund University 10 days after hatching where they were fed live copepods and cladocerans once a day. After 7 weeks, pike were moved to net cages to prevent cannibalism and 3 weeks prior to the fish prey trials, pike were fed live juvenile roach once per day. All fish were kept in clear water at a temperature of 18–20 °C and in fluorescent light (GE Lighting Polylux XLR, 85Wx2, GE Lighting, Cleveland, OH, USA) in 12:12 hour light/dark cycles which was gradually changed to 14:10 hour light/dark cycles during spring and early summer to mimic the natural photoperiod.

Turbid water was obtained using green algae with a dominance of *Scenedesmus* spp. that were allowed to grow to high densities, whereas DOM water was collected from a nearby pond (Black pond, Frihult, 55°33′N, 13°39′E). The turbid and DOM water was diluted to a visual range of 25 cm (turbid water chl *a*, 705 $\mu g \cdot L^{-1}$; and DOM water $abs_{420/1}$, 0.32). The visual range in the water was defined as the horizontal distance between the human eye and a Secchi disc at which the contrast between the disc's black and white fields disappeared. This method has been previously used (Jönsson et al. 2011a,b), and evaluation of the method has shown that reaction distance of adult pike feeding on fish prey is tightly correlated to this measure of visual range (Ranåker, L., Jönsson, M., Nilsson, P. A. and Brönmark, C. unpublished data). Visual range refers to our measured visual range, and when the actual distance the fish can see in the water is referred to in the text, reaction distance is used instead. To create diffuse light conditions, two halogen spotlights (150 W each) illuminated the arenas from above through white fabric. Halogen light bulbs were used to ensure that a broad spectrum of light was present (λ, 410–930 nm). Most wavelengths were also present at the bottom in all treatments owing to the shallow depth (λ, 420–930 nm in algal turbid water and 460–930 nm in brown water, Ocean Optics HR4000 high-resolution spectrometer, Ocean Optics, Dunedin, FL, USA), and the composition of the light included the absorption peak in the eyes of both pike (λ, approximately 525 nm) and roach (λ, approximately 530 nm (Jokela-Määttä et al. 2007). Light levels during trials were 111 lux at the water surface, which corresponds to early dawn and late dusk levels, and 105, 76 and 45 lux at the bottom in clear, turbid and DOM water, respectively (INS DX-100 Digital lux meter, INS Enterprise, Taipei, Taiwan). The intensity of PAR (photosynthetically active radiation) was 2.33 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the surface and 2.04, 1.42 and 0.93 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the bottom in clear, turbid and DOM water, respectively, and the level of UVA radiation was 1.99 $\mu W \cdot cm^{-2}$ at the surface and 1.67, 1.45 and 1.24 $\mu W \cdot cm^{-2}$ at the bottom in clear, turbid and DOM water, respectively [NIST Traceable radiometer and photometer, International Light IL1400A (International Light Technologies, Peabody, MA, USA) with both PAR and UV sensors]. The water depth was 6.0 cm, which is the depth that all light measurements were taken, in all trials except reaction distance trials where it was 2.0 cm to make the arena as two dimensional as possible. Light was not measured at 2.0 cm depth as the shallower depth will affect the light less than the 6.0 cm depth will. All trials were recorded with cameras from above for later analysis. After all trials, photographs of the fish were taken for the measurement of total length in Motic Images Plus 2.0ML (Motic Group, Xiamen, China). However, photographs of prey fish were taken before trials. The duration of trials was determined in pre-trials so that they were long enough to ensure fish feeding but short enough to avoid satiation.

Roach foraging trials

Foraging trials with roach [roach total length (L_T), 15.5 ± 1.9 mm, mean ± SD; age, 5 weeks] foraging on copepods (eight replicates) were performed in square arenas (15.4 × 18.0 cm), and where roach (roach L_T, 19.8 ± 2.0 mm; age, 9 weeks) were foraging on *Daphnia* (seven replicates), circular arenas (Ø 45 cm) were used. Larger arenas were used as the roach feeding on *Daphnia* had grown to a larger size. Each trial was performed with a group of three roach, acclimatised for 30 min prior to experimentation. Groups were used to minimise stress as roach is a shoaling species. Trials were started by adding 40 copepods or *Daphnia* in the centre of the arena, lasted 30 min with copepod prey and 5 min with *Daphnia* as prey, and were terminated by removing the three roach. The water was then filtered through a 50-μm plankton net, and remaining copepods or *Daphnia* were counted. Roach and prey individuals were used only once in experiments, and only consumption was evaluated as separate foraging cycle components in roach are difficult to quantify owing to roach and zooplankton sizes. Further, activity and swimming pattern were not quantified because of technical limitations in the software used (Noldus EthoVision, version 3.1, Noldus Information Technology, Wageningen, Netherlands). Proportions of zooplankton consumed were arcsin$\sqrt{x}$-transformed before statistical analyses by ANOVA to satisfy the assumptions of normality and homoscedasticity, but figures show absolute consumption.

Pike reaction distance

Experiments on pike reaction distance to *Daphnia* as prey (seven, eight and five replicates for clear, turbid and DOM water, respectively) were performed in a circular arena (Ø 16 cm). One pike (L_T, 17.3 ± 0.8 mm; age, 4 weeks) was acclimatised for 10 min before the trials were started by releasing five *Daphnia* into the arena. Reaction distance was quantified as the distance between the snout of the pike and the nearest body part of the prey when pike turned its head or the entire body towards the prey. All pike and *Daphnia* were used only once, but in trials with roach as prey (roach L_T, 18 mm), pike had reached a size that allowed more handling (pike L_T, 54.4 ± 2.9 mm; age, 9 weeks), and the pike individuals were hence subjected to all treatments in a randomised order. These trials were performed in larger rectangular arenas (24 × 44 cm) as the reaction distance to larger prey is greater. Roach were placed in a cylinder-shaped glass container (Ø 3.0 cm) inside the arena to prevent pike from using other senses than vision for prey detection, and reaction distance was defined as above. No acclimatisation of pike was necessary as they immediately engaged in prey searching behaviour, and all fish were measured (nearest mm) after trials. Differences in reaction distance with *Daphnia* as prey were evaluated by ANOVA. With roach as prey, a randomised block ANOVA was used with individual pike as the blocking factor that controls for potential differences between pike individuals and reduces the degrees of freedom according to the experimental design (Quinn & Keough 2002).

Pike foraging trials

All pike trials were performed in circular arenas (Ø 45 cm) with a single pike each time. With *Daphnia* as prey (six replicates), each pike (pike L_T, 38.3 ± 3.2 mm; age, 6 weeks) was acclimatised in the arenas for 30 min before trials were started by releasing 40 *Daphnia* in the centre of the arena. Trials were terminated after 10 min by removing the pike, and the water was then filtered through a 50-μm plankton net and remaining *Daphnia* were counted. Pike and *Daphnia* were used only once. In the trials with roach as prey (roach L_T, 19.2 ± 1.9 mm), the same pike used for the quantification of reaction distance were used and were subjected to all treatments in a randomised order (seven replicates). Pike were acclimatised in the arenas for 30 min before trials were started, and 5 min before trial start, 10 roach were released into a net cage in the centre of the arena to allow them to acclimatise to experimental conditions. Trials were started by removing the net cage and were terminated after 30 min by removing the pike. Remaining roach were counted. Activity (total distance moved and time spent moving) and swimming pattern (turn rate or tortuosity, which is the degree of turn per distance moved) were obtained using Noldus EthoVision, version 3.1 for Windows. In addition to consumption rate, attack rate (number of attacks during trial time) and capture success (proportion of the attacks that resulted in consumption) were also quantified. In the *Daphnia* experiment, consumption was evaluated as the $\arcsin\sqrt{x}$-transformed proportion of *Daphnia* consumed, but figures show absolute consumption. In the roach prey experiment, time to first capture was used as a measure of consumption rate in order to satisfy the assumption of a continuous response variable, as very few roach were consumed. Differences in the dependent variables total distance moved, time spent moving, turn rate, attack rate, capture success and consumption rate with *Daphnia* as prey were evaluated using MANOVA. In the roach prey experiment, a randomised block MANOVA with pike individual as the blocking factor was used. All statistics were performed in IBM SPSS Statistics 19.0 for Windows (IBM, Armonk, NY, USA).

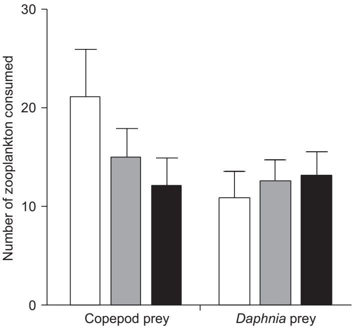

Fig. 1. Consumption of copepods by 5-week-old roach (L_T, 15.5 ± 1.9 mm, mean ± SD) and consumption of *daphnia* by 9-week-old roach (L_T, 19.8 ± 2.0 mm) in clear (open bar), algal turbid (grey bar) and water coloured brown by dissolved organic matter (DOM; black bar). The visual range in algal turbid and DOM water was 25 cm. Statistical significance is indicated with stars, and error bars denote one SE.

Results

There was no effect of visual conditions on consumption rates in roach (Fig. 1) for either of the two prey types, copepods ($F_{2,21} = 1.62$, $P = 0.222$) and *Daphnia* ($F_{2,18} = 0.25$, $P = 0.782$).

There was a marginally significant effect of visual conditions on the reaction distance of pike feeding on *Daphnia* ($F_{2,17} = 34.32$, $P = 0.056$). When feeding on YOY roach, there was no difference between individual pike in reaction distance ($F_{7,14} = 1.426$, $P = 0.270$), but there was a significant effect of visual conditions ($F_{2,14} = 14.797$, $P < 0.001$) with longer reaction distances in clear (24.2 ± 9.1 cm) than in turbid ($P = 0.007$, 13.6 ± 5.1 cm) and DOM water ($P < 0.001$, 8.7 ± 2.7 cm, Fig. 2). However, there was

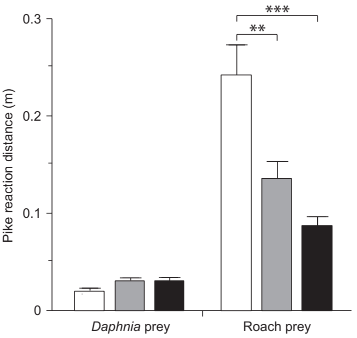

Fig. 2. Reaction distance of 4-week-old pike (L_T, 17.3 ± 0.8 mm, mean ± SD) to *Daphnia* and 9-week-old pike (L_T, 54.4 ± 2.9 mm) to roach (L_T, 18 mm) in clear (open bar), algal turbid (grey bar) water coloured brown by dissolved organic matter (DOM; black bar). The visual range in both visually degraded treatments was 25 cm. Stars indicate statistical significance, and error bars denote one SE.

no difference between DOM and turbid water ($P = 0.253$).

For pike feeding on *Daphnia*, there was no effect of visual conditions on total distance moved (Fig. 3a), time spent moving (Fig. 3b), turn rate (Fig. 3c), attack rate (Fig. 4a), capture success (Fig. 4b) or consumption rate (Fig. 4c, Wilk's $\lambda = 0.446$; $F_{12,20} = 0.828$; $P = 0.623$). However, in the experiments when pike fed on YOY roach, we found a significant overall effect of visual conditions on pike foraging behaviour (Wilk's $\lambda = 0.098$, $F_{12,14} = 2.563$, $P = 0.048$), and there was also a significant block effect indicating differences between individual pike (Wilk's $\lambda = 0.004$; $F_{36,33.5} = 2.395$; $P = 0.006$). As the effect of visual condition was significant in the MANOVA, we proceeded with evaluating the univariate between-subject effects. There was a significant effect on attack rate (Fig. 4a, $F_{2,12} = 7.825$; $P = 0.007$), with lower attack rates in clear than in turbid ($P = 0.008$) and DOM water ($P = 0.023$), respectively. However, there was no difference in attack rate between turbid and DOM water ($P = 0.833$). There were also marginally significant effects for turn rate (Fig. 3c, $F_{2,12} = 3.711$; $P = 0.056$) and capture success (Fig. 4b, $F_{2,12} = 3.162$; $P = 0.079$), with higher turn rate in DOM compared to turbid water ($P = 0.048$) and higher capture success in clear compared to turbid water ($P = 0.067$). Total distance moved (Fig. 3a, $F_{2,12} = 0.579$; $P = 0.576$), time spent moving (Fig. 3b, $F_{2,12} = 1.436$; $P = 0.276$) and consumption rate (Fig. 4c, $F_{2,12} = 2.281$; $P = 0.145$) were not affected by visual conditions.

Discussion

The present work shows that zooplanktivory in a juvenile planktivore is unaffected by naturally occurring levels of turbidity and DOM. However, for a visual piscivore, the reaction distance to both plankton and fish prey is affected. When foraging on fish prey

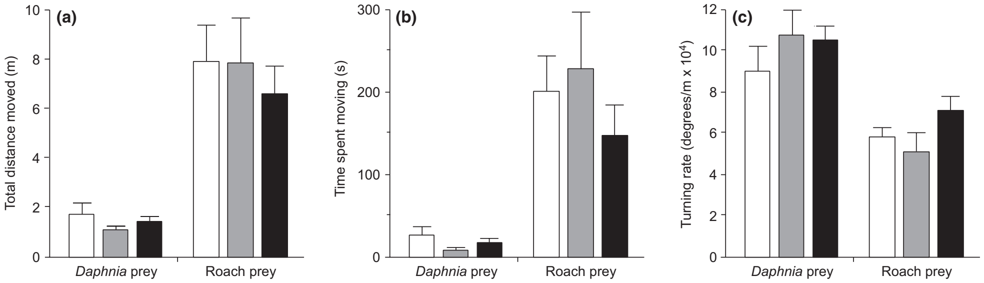

Fig. 3. Distance moved (a), time spent moving (b) and turn rate (degree of turn per distance moved, (c) of 6-week-old pike (L_T, 38.3 ± 3.2 mm, mean ± SD) foraging on *Daphnia* and 9-week-old pike (L_T, 54.4 ± 2.9 mm) foraging on roach (L_T, 19.2 ± 1.9 mm) in clear (open bar), algal turbid (grey bar) and water coloured brown by dissolved organic matter (DOM; black bar). In algal turbid and DOM water, the visual range was 25 cm. Error bars denote one SE, and statistical significance is indicated with stars.

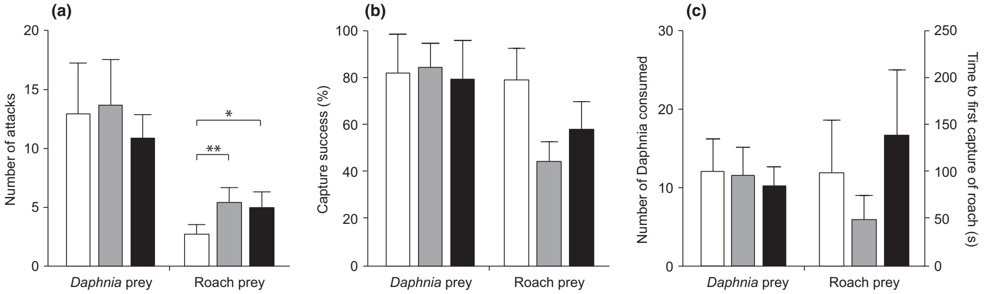

Fig. 4. Attack rate (number of attacks performed, (a), capture success (proportion of attacks that resulted in ingestions), (b) and consumption rate (number of *Daphnia* consumed and time to first capture of roach, (c) of 6-week-old pike (L_T, 38.3 ± 3.2 mm, mean ± SD) foraging on *Daphnia* and 9-week-old pike (L_T, 54.4 ± 2.9 mm) foraging on roach (L_T, 19.2 ± 1.9 mm) in clear (open bar), algal turbid (grey bar) and water coloured brown by dissolved organic matter (DOM; black bar). Algal turbid and DOM water had a visual range of 25 cm. Statistical significance is indicated with stars, and error bars denote one SE.

especially, reaction distance is severely reduced. This reduction in reaction distance would decrease the encounter rates with prey if it is not counteracted by an increase in foraging effort, which is seen as an increased attack rate in visually degraded water. However, pike do not compensate for the reduction in reaction distance by increasing its swimming activity. Also, these effects on YOY fish are similar regardless of the type of agent causing the visual degradation.

For prey detection to occur, the projection of the prey on the retina of the forager has to be large enough, and the size of the projection is determined by the size of the prey and its distance from the forager (Aksnes & Giske 1993). Small prey have to be closer to the forager to be detected, and therefore, the effects of visual conditions on foraging is predicted to increase in strength as prey size increases (Vinyard & O'brien 1976; Chesney 1989; De Robertis et al. 2003). There are also other factors affecting detection of prey like contrast (Lythgoe 1979; Utne-Palm 2002) and movements of the prey (Utne-Palm 1999). The different prey types used in this study differ in most of these parameters which somewhat confounds the mechanistic analysis, but they were chosen to resemble the prey types utilised in natural systems at the specific age or size of the forager. For roach, we were unable to determine reaction distance as they did not react very clearly when they detect prey. For pike, on the other hand, the response is very distinct both for plankton and for fish prey. In clear water, the reaction distance of YOY pike to *Daphnia* was 2.0 cm, indicating that a reduction in visual range from clear water to a visual range of 25 cm would not restrict the reaction distance of pike (Fig. 2). In accordance with the predictions, the visually degraded treatments did not restrict reaction distance but instead enhanced it (Fig. 2). This has previously been shown in clay turbid water where enhanced prey contrast has been proposed as the likely explanation (Hinshaw 1985; Gregory & Northcote 1993). It is uncertain whether this increase in reaction distance (2.0–3.1 cm) is of ecological relevance as there were no effects on any of the foraging parameters analysed. These limited effects of visual conditions may also partly be due to the developmental stage of the fish eyes. Pike were only 17.3 mm long at the age of 4 weeks when the trials were performed, and it is likely that the eyes were not fully developed at that age. However, increasing the size of the prey changes the prerequisites for detection and thereby also the predictions.

The reaction distance of YOY pike to roach prey was severely affected by reductions in the visual range with reductions both in DOM (64%) and in turbid water (44%). Reaction distance in clear water was 24.2 cm, which can be considered the maximal visual ability of pike at that size and light condition. In both DOM and turbid water, the visual range was 25 cm, which resulted in severely reduced reaction distance even if it was greater than pike's maximal visual ability (Fig. 2). Reductions in visual range may therefore affect juvenile fish even if the visual range is greater than their maximal reaction distance. As the reaction distance is reduced with visual degradation, the search efficiency (volume of water searched per unit of time) of the forager is also reduced. Calculating the water searched at any instant by the forager as a spherical sector (cone with a spherical end) with the reaction distance as the radius and a horizontal visual field angle of 150° (Raat 1988) reveals that search volume is substantially reduced in both DOM (95%) and turbid water (82%), which will reduce the probability of encountering prey. Pike counteracted the decrease in search efficiency by increasing the attack rate (Fig. 4a), which together with a trend towards decreasing capture success (Fig. 4b) resulted in no difference in consumption (Fig. 4c). The reduced capture success may be due to lower precision in the attacks as the visual information available to the forager is reduced. Even if prey are detected, the image quality may still be affected. Image degradation may lower the ability of the predator to estimate size, swimming ability and condition of prey within the reaction distance, resulting in predators not being able to efficiently select the desired prey (Abrahams & Kattenfeld 1997; Reid et al. 1999). Despite the large reduction in search volume, there was no effect of visual conditions either on distance moved (Fig. 3a) or on how much time they spend moving (Fig. 3b). Increased movement exposes juvenile pike to larger predators, both to other species and to cannibalistic conspecifics, more than increased attack rates would, possibly making this strategy more beneficial in communities with high predation risk or intracohort cannibalism, which often is the case in dense pike populations (Raat 1988). Further, there was a trend towards a higher turn rate in DOM water (Fig. 3c), but having a high turn rate *per se* does not increase the search efficiency as turning would induce more overlap in the water volume searched. Also, this increased turn rate was not present in turbid water, making orientation issues linked to low light intensities a more likely explanation.

At high prey density, encounter rates with prey may still be high enough to satisfy the predator even under deteriorated visual conditions. However, at low prey density, the probability to encounter prey may not be sufficient to sustain foraging rates. Here, YOY fish are affected similarly by DOM and turbid water, but in natural systems, DOM and turbid water systems are very different. Algal turbid waters especially are generally eutrophic, with high densities of juvenile fish and abundant food resources, resulting in high encounter rates for foragers. The high prey density therefore buffers the negative effects of visual degradation, and a high consumption rate may be sustained. In DOM water, the availability of light limits the productivity and prey density is low (Karlsson et al. 2009). Visual degradation is therefore likely to have disproportionately large effects on foraging in fish in systems rich in DOM. Further, even if the reasons for increased concentrations of DOM in aquatic environments are still under debate, hydrology and flow regime seem to be important factors (Erlandsson et al. 2008) that may increase in the Northern Hemisphere the coming decades because of climate change (IPCC 2007). Increased DOM concentration may lead to increased sensitivity of lakes in general and strengthen the effects of visual constraints on fish foraging.

This study provides empirical evidence that even if YOY fish foraging on zooplankton may not be affected by visual degradation, YOY piscivorous fish are affected. This effect is present even if the visual range in the water is not reduced below the maximum reaction distance of the fish. Reduced search efficiency was counteracted by increased attack rate but not activity, which may be beneficial in high-risk environments where increased movement would increase exposure to predation. As pike consumption rates were not affected by visual degradation, they were able to efficiently counteract the decreased search efficiency by increasing the attack rate. Also, the effects of visual degradation on foraging in YOY fish are similar, regardless of whether the water is turbid or coloured by DOM. There is a potential of these effects becoming more pronounced in future through a continued increase in DOM concentration of aquatic ecosystems because of changing climatic conditions. Therefore, there is a need for further estimations of the sensitivity of aquatic ecosystems differing in trophic status but nevertheless similarly subjected to increasing brown coloration and thereby visual degradation.

Acknowledgements

We thank Jan Morén and the Fishing Preservation District of Lake Bäsingen, Sweden, for hatching and providing larval pike and the Swedish Research Council Formas for funding the project. Experiments were approved by an ethical committee (Dnr M165-07), and facilities have permits for fish husbandry from the Swedish Board of Agriculture (Dnr 35-1878/03).

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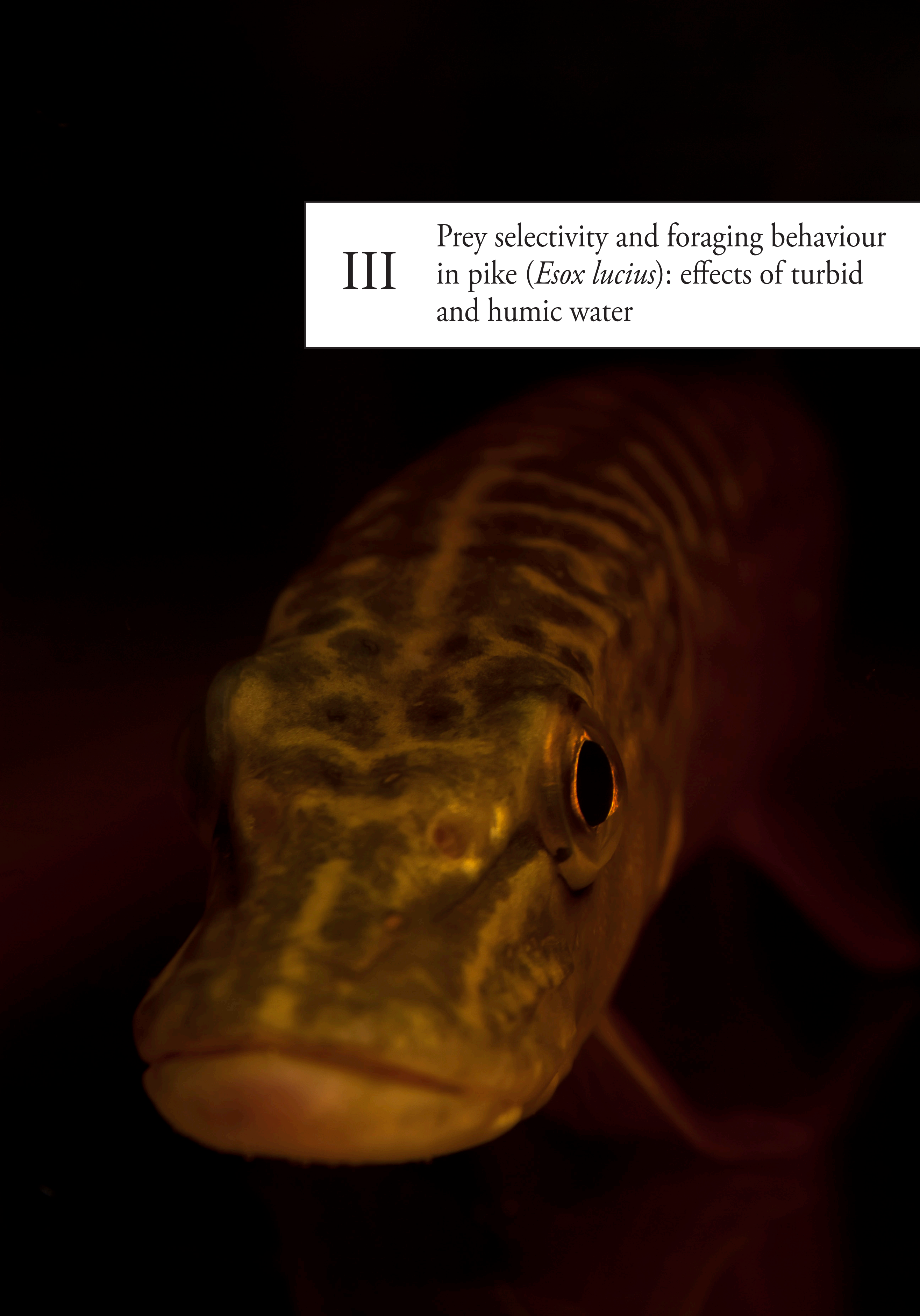
III

Prey selectivity and foraging behaviour in pike (*Esox lucius*): effects of turbid and humic water



Prey selectivity and foraging behaviour in pike (*Esox lucius*): effects of turbid and humic water

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Abstract

Predators are known to exert a strong regulating force on lower trophic levels trough predation and as most aquatic piscivores are visual foragers, the visual conditions in the water have the potential to alter the strength of these regulating forces. We evaluate the effects of turbidity and humic water coloured brown by dissolved organic matter (DOM), which have completely different optical properties, on prey size selectivity and foraging efficiency in the visual piscivore pike (*Esox lucius*) feeding on roach (*Rutilus rutilus*). Prey size selectivity towards small prey in clear water collapses in turbid water while it is maintained in humic water due to that humic water absorbs light instead of scattering it which maintains image quality. Encounter rates decrease similarly in both turbid and humic water but is not counteracted by increased searching activity. Capture success is not affected by turbidity but is affected by humic water. Capture success is high in clear water and in high DOM but low in low DOM. In low DOM pike may be detected by its prey at a distance but in high DOM, the visual range approaches the pike´s strike distance and in combination with low contrast between the dark green pike and the brown background, pike may be able to initiate an attack before it is detected by the prey, severely limiting the possibility for the prey to perform evasive manoeuvres. We show that the type of visual degradation affects foraging in a visual piscivore differently which have not previously been acknowledged in the visual foraging literature.

IV

Clear-water conditions increase perch (*Perca fluviatilis*) growth regardless of prey density in a biomanipulated lake

CLEAR-WATER CONDITIONS INCREASE PERCH (*PERCA FLUVIATILIS*) GROWTH REGARDLESS OF PREY DENSITY IN A BIOMANIPULATED LAKE

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Abstract

Visual conditions have complex effects on foraging in fish, including behavioural changes in both predator and prey, making it difficult to estimate the overall effect of visual conditions on piscivorous predators. By using biomanipulated lakes where the whole lake have been manipulated to change the visual conditions and prey density, the overall effect on predators can be evaluated through their individual growth rate. In Lake Finjasjön, length at age for a visual piscivore, perch (*Perca fluviatilis*), increased after biomanipulation when Secchi depth increased from 0.35 to 1.16 m even though relative prey density and biomass decreased 10-fold. Visual conditions completely counteracted the negative effects of reduced prey density making visual conditions more important in regulating foraging gain in a visual piscivore. The removal of large parts of the planktivorous fish guild, through biomanipulation, does not reduce the growth of the more desirable piscivorous species, often targeted by recreational angles, but instead increase it substantially. The ecosystem services that these lakes provide, in respect to fish production and recreational value, may therefore be maintained.

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Departement of Biology
Aquatic Ecology
ISBN 978-91-7473-299-3
Printed by Media-Tryck, Lund 2012

ISBN 978-91-7473-299-3