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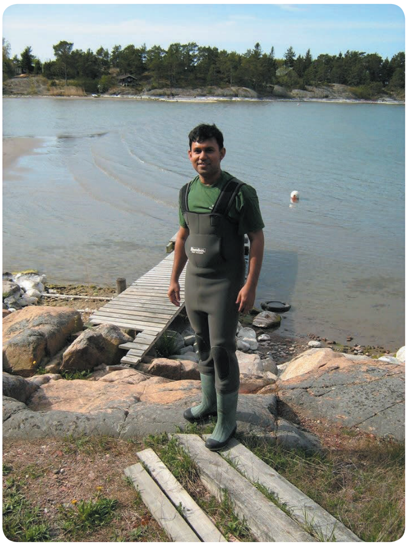
Effects of algal turbidity on foraging and antipredator behaviour of the three-spined stickleback (*Gasterosteus aculeatus*)



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EFFECTS OF ALGAL TURBIDITY ON FORAGING AND ANTIPREDATOR BEHAVIOUR OF THE THREE-SPINED STICKLEBACK (*GASTEROSTEUS ACULEATUS*)

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Environmental and Marine Biology

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I. M. J. Ajemian., **S. Sohel.**, J. Mattila (2015) Effects of turbidity and habitat complexity on antipredator behavior of three-spined sticklebacks (*Gasterosteus aculeatus*). Environmental Biology of Fishes 98(1), 45-55

II. **Shakwat Sohel**, Kai Lindström (2015) Algal turbidity reduces risk assessment ability of the three-spined stickleback. Ethology121, 548-555

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IV. **Shakwat Sohel**, Sami Merilaita, Kai Lindström. Increased turbidity causes a mismatch between the distribution of social foragers and their resource. (Manuscript)

CONTRIBUTION OF AUTHORS:

I. **Sohel** and Ajemian designed the study together with Mattila. **Sohel** and Ajemian were responsible for behavioural experiments, data collection and video analysis. Data analysis was done by Ajemian and **Sohel** wrote the manuscript. Mattila contributed with comments.

II. **Sohel** designed the study and was responsible for behavioural experiments, data collection, video analysis and manuscript preparation. Lindström contributed with data analysis and writing the manuscript.

III. **Sohel** and Lindström designed the study. **Sohel** was responsible for behavioural experiments, data collection and video analysis. Mattila contributed with logistics and counselling during the experiments. Data analysis was done by Lindström. **Sohel**, Mattila and Lindström wrote the manuscript.

IV. The study was designed by Lindström and **Sohel**. **Sohel** was responsible for behavioural experiments, data collection and video analysis. Lindström analysed the data. **Sohel**, Merilaita and Lindström wrote the manuscript.

ABSTRACT

The aim of this thesis was to examine how aquatic organisms, such as fish, behave in an altered environmental condition. Many species of fish use vision as their primary tool to gain information about their surrounding environment. The visual conditions of aquatic habitats are often altered as a result of anthropogenic disturbance, such as eutrophication that initiates algal turbidity. In general, turbidity reduces the visibility and can be hypothesized to have an influence on the behaviour of fish. I used the three-spined stickleback (*Gasterosteus aculeatus*) as a model species and conducted four studies in the laboratory to test how algal turbidity affects its behaviour.

In this thesis, two major behavioural aspects are discussed. The first is antipredator behaviour. In study **I**, the combined effects of turbidity and shoot density on habitat choice (shelter vs open) behaviour was tested on a group of sticklebacks (20 fish) in the presence and absence of piscivorous perch (*Perca fluviatilis*). In study **II**, I examined the behavioural responses of feeding sticklebacks when they were exposed to the sudden appearance of an avian predator (the silhouette of a common tern, *Sterna hirundo*). The study was done in turbid and clear water using three different groups sizes (1, 3 and 6 fish).

The second aspect is foraging behaviour. Study **III** & **IV** focused on the effects of algal turbidity on the foraging performance of sticklebacks. In study **III**, I conducted two separate experiments to examine the effects of turbidity on prey consumption and prey choice of sticklebacks. In this experiment turbidity levels and the proportion of large and small prey (*Daphnia* spp.) were manipulated. In study **IV**, I studied whether a group of six sticklebacks can distribute themselves according to food input at two feeding stations in a way that provided each fish with the same amount of food in clear and turbid water. I also observed whether the fish can follow changes in resource distribution between the foraging patches.

My results indicate an overall influence of algal turbidity on the antipredator and foraging behaviour of sticklebacks. In the presence of a potential predator, the use of the sheltered habitat was more pronounced at higher turbidity. Besides this, sticklebacks reduced their activity levels with predator presence at higher turbidity and shoot density levels, suggesting a possible antipredator adaptation to avoid a predator.

When exposed to a sudden appearance of an avian predator, sticklebacks showed a weaker antipredator response in turbid water, which suggests that turbidity degrades the risk assessment capabilities of sticklebacks. I found an effect of group size but not turbidity in the proportion of sticklebacks that fled to the shelter area, which indicates that sticklebacks are able to communicate among group members at the experimental turbidity levels.

I found an overall negative effect of turbidity on food intake. Both turbidity and changes in the proportion of prey sizes played a significant role in a stickleback's prey selection. At lower turbidity levels (clear <1 and 5 NTU) sticklebacks showed preferences for large prey, whereas in more turbid conditions and when the proportion of large to small prey increased sticklebacks became increasingly random in their prey selection. Finally, my results showed that groups of sticklebacks disperse themselves between feeding stations according to the reward ratios following the predictions of the ideal free distribution theory. However, they took a significantly longer time to reach the equilibrium distribution in turbid water than in clear water. In addition, they showed a slower response to changes in resource distribution in a turbid environment. These findings suggest that turbidity interferes with the information transfer among group foragers.

It is important to understand that aquatic animals are often exposed to a degraded environment. The findings of this thesis suggest that algal turbidity negatively affects their behavioural performance. The results also shed light on the underlying behavioural strategies of sticklebacks in turbid conditions that might help them adapt to an altered environmental situation and increase their survival. In conclusion, I hold that although algal turbidity has detrimental effects on the antipredator and foraging behaviour of sticklebacks, their behavioural adjustment might help them adapt to a changing environment.

Keywords: turbidity, eutrophication, predator avoidance, optimal foraging, diet selection, schooling, ideal free distribution, social foraging, public information

SAMMANFATTNING

Avsikten med detta arbete var att undersöka hur fiskars beteende påverkas av förändrade miljöförhållanden. Många fiskarter använder synen för att samla information om sin omgivning. Samtidigt är akvatiska miljöer ofta utsatta för störningar av antropogent ursprung, som påverkar vattnets visuella egenskaper. Ett exempel är eutrofieringen, som är en av de viktigaste orsakerna till ökad grumlighet. Grumlighet orsakar siktförsämring och kan därför förväntas påverka fiskars beteende. I mitt arbete har jag använt storspiggen (*Gasterosteus aculeatus*) som modellsystem, och utfört fyra olika delarbeten för att undersöka hur grumlighet orsakad av algblomning påverkar spiggens beteende.

Min avhandling fokuserar på två kategorier av beteenden, som är viktiga för individens överlevnad. Den första kategorin är hur predatorer undviks. I delarbete **I** undersöktes hur grumlighet och vegetation påverkar spiggarnas val av habitat (skydd eller öppet) i frånvaron och närvaron av en abborre (*Perca fluviatilis*). Spiggarna testades i grupper om 20 fiskar. I delarbete **II** undersöktes beteenderesponsen till en attackerande modell av en fisktärna (*Sterna hirundo*). Detta gjordes både i klart och grumligt vatten. Beteendet testades för enskilda fiskar och grupper om 3 och 6 fiskar.

Den andra kategorin av beteende är näringssök. Hur grumlighet påverkar furageringbeteendet testades i delarbetena **III** och **IV**. I delarbete **III** utförde jag två separata experiment, som testade hur grumligheten påverkar näringsintaget och valet av byte hos enskilda spiggar. I dessa experiment manipulerades grumligheten och proportionen av små och stora bytesdjur (*Daphnia* spp.). Delarbete **IV** undersökte huruvida spiggarna, som furagerade i grupper om 6 fiskar, kunde erhålla information om varandras furageringsframgång i grumligt vatten. Detta gjordes genom att observera hur fiskarna fördelade sig mellan två näringskällor med olika belönings-grad. Jag observerade också om grumligheten påverkade spiggarnas förmåga att följa förändringar i belönings-graden.

Mina resultat visar tydligt att storspiggens förmåga att undvika predatorer och söka näring påverkas av grumlighet. I närvaron av en predator, i grumligt vatten, använde sig fiskarna av det skyddade habitatet i mycket högre grad än i klart vatten. Dessutom så minskade fiskarna på sin aktivitet i grumligare vatten och i tätare vegetation. Detta kan utgöra en anpassning för att undvika predation. När spiggarna exponerades för en plötslig attack

från luften, så uppvisade den en klart mindre utvecklad flyktrespons i grumligt än i klart vatten. Andelen spiggar som flydde in i det skyddade habitatet påverkades av gruppstorleken, men inte grumligheten. Detta antyder att kommunikationen mellan fiskarna inom gruppen inte helt omöjliggjordes av de använda grumlighetsnivåerna.

Grumlighet hade en generell negativ effekt på fiskarnas näringsintag. I grumligt vatten lyckades de fånga färre byten. Både graden av grumlighet och proportionen av små och stora byten hade en effekt på spiggarnas val av byte. Vid låg grumlighet (klart vatten till 5 NTU) uppvisade spiggarna en preferens för stora byten. Denna preferens försvann och utbyttes mot ett slumpmässigt val av byte när grumligheten ökade och när andelen stora byten ökade. Mina resultat visade att spiggarna kan fördela sig på två olika näringskällor enligt belönings-graden, så att varje fisk kan förvänta sig en lika stor belöning. Det tog dem dock en betydligt längre tid att fördela sig i grumligt än klart vatten. När belönings-graden förändrades, var spiggarna i grumligt vatten betydligt långsammare och sämre på att hitta det nya balansläget. Dessa resultat visar tydligt att grumligheten stör utbytet av information mellan gruppmedlemmarna i ett fiskstim.

Det är viktigt att inse att akvatiska organismer ofta är utsatta för försämrade miljöer. Resultaten i denna avhandling visar tydligt att grumlighet orsakad av algblomning kan ha en negativ effekt på fiskars förmåga att undvika predatorer och hitta och inta näring. Resultaten belyser också beteenden, som kan hjälpa storspiggen att anpassa sig till en förändrar miljö.

Nyckelord: grumlighet, eutrofiering, predation, optimal furagering, födoval, stim, fördelning av individer, socialt födosök, offentlig information

1. INTRODUCTION

Most organisms interact with their environment through different behavioural responses. A common view is that behaviour acts as a bridge between an organism and its surroundings. Often changes in the surrounding environment may affect an organism´s natural behaviour. Most animals monitor their environment constantly and sometimes they need to alter their behavioural response as a survival strategy with a changing environmental condition. Typically animals base their behaviour upon their own sensory system to acquire information regarding these changes. A change in the behaviour of an animal can often be the first clue of environmental degradation. For example, if somebody waits until populations are declining in a particular area, then it may be too late to take measures to save the population. Thus, regular monitoring of the natural behaviour of different organisms in their natural habitat is vital to provide baseline data for future environmental monitoring.

This thesis focuses on the foraging and antipredator behaviour of three-spined sticklebacks under algal turbidity. Algal turbidity is a common phenomenon in many aquatic environments and is typically a consequence of human induced eutrophication. Several studies show that turbidity alters the behaviour of fish (Andersen et al. 2008, Engström-Öst & Mattila 2008, Ferrari et al. 2010), but the underlying reasons for these changes are less understood. It is important to observe the effects of algal turbidity on foraging and antipredator behaviour of fish in order to understand the impacts of environmental degradation due to the eutrophication process. At the same time, such observations will reveal potential adaptations of fish to such degraded environmental conditions.

1.1 Eutrophication and algal turbidity

Eutrophication results from *"an increase in the rate of supply of organic matter to an ecosystem"* (Nixon 1995). Due to eutrophication the productivity of many aquatic ecosystems has increased resulting in mass production of algae that suffocate vegetation, deplete oxygen and increase turbidity (Valiela et al. 1997, McGlathery 2001, Cloern 2001). Algal turbidity has become a frequent phenomenon of many shallow aquatic areas in the last decades (Sanden & Håkansson 1996; Dupont & Aksnes 2013). Recently, Selman et al. (2008) recorded 415 eutrophic coastal systems around the globe, which indicates that this is a pronounced global problem.

Fish mostly depend on vision as their main source of sensory information (Guthrie & Muntz, 1993), although in general, they are always surrounded by poor quality underwater images. Turbidity decreases underwater visibility by increasing light attenuation that eventually decreases light penetration and reduces apparent contrast (Kirk 1985). Several studies indicate that elevated turbidity might play a significant role in affecting different behaviours of fish. These include parental care (Järvenpää & Lindström 2011), mate choice (Sundin et al. 2010), nest construction (Wong et al.2012) and sexual selection (Järvenpää & Lindström 2004; Candolin et al. 2007). Thus, it is possible that animals facing increased turbidity may respond to these altered conditions via new behavioural patterns which have been less explored.

1.2 Turbidity-effects on prey consumption

There is a general consent that turbidity affects predator-prey interactions in fish communities (Gregory 1993, Zamor & Grossman 2007, Shoup & Wahl 2009). Some studies have measured the reactive distance to determine the effects of turbidity on feeding success and found that the reaction distance decreases with increasing turbidity (Vinyard & O´Brien 1976, Gregory & Northcote 1993, Miner & Stein 1993, Utne-Palm 1997). This results in a decreased feeding efficiency (De Robertis et al. 2003, Nurminen & Horppila 2006), although some studies showed no significant reductions in the consumption of prey with increased turbidity (Reid et al. 1999; Granqvist & Mattila 2004). However, other studies showed enhanced foraging success with increasing turbidity (Gregory & Northcote 1993). An example of this is shown when the highest feeding rates of juvenile chinook salmon (*Oncorhyncus tshawytscha*) occurred at turbidity levels of 35-100 NTU, probably because of the possible decrease in predator risk in turbid condition (Gregory 1993). Similarly in the presence of predators, fathead minnows (*Pimephales promelas*) increased their feeding in turbid water (Abrahams & Kattenfeld 1997). The contrast between a prey and its background increases at intermediate turbidity levels, and because of this some fish species are able to reach a higher feeding rate at medium turbidity levels (Utne-Palm 1999). Therefore, it seems that depending on species and life stages, turbidity can have both positive and negative effects on different foraging aspects of visual foragers (reviewed by Utne-Palm 2002). The assessment of both antipredator and foraging behaviour in elevated turbidity will clarify the effects of turbidity on predator-prey interaction as well as prey consumption.

1.3 Turbidity-effects on antipredator behaviour

Small teleost fish typically have a high risk of being preyed upon and face a constant threat of predation from several potential predators (Lima & Dill 1990, Schmitz 2007). Predator defence largely depends on a prey fish´s ability to evaluate and respond appropriately towards specific predatory actions. Particularly, a fish is at risk from a sudden ambush predator or bird predator when foraging, because concentration on food handling can impair the individual's ability to monitor its surrounding for predators. In such a situation, early detection of an approaching predator could assist the prey fish to escape.

Exposure to predators generates different types of behaviour in prey. In the presence of a predator, fish often move from an open habitat to a more sheltered habitat (Werner et al. 1983, Gotceitas & Brown 1993). Dense vegetation serves as a physical or visual barrier (Shoji et al. 2007) and reduces encounter rates with predators as well as foraging efficiency of predators (Savino & Stein 1989, Mattila 1992). It should be noted that different types and density of vegetation have species and size specific influence on different antipredator behaviour of prey fish (Chick & McIvor, 1997). The decision whether to initiate antipredator behaviour requires accurate and reliable information regarding a possible predation threat (reviewed by Kats & Dill 1998). In general, fish obtain such information through environmental cues that are detected and processed by their three major sensory organs: vision, olfaction and lateral line system (Pitcher, 1986). As the ability to use vision decreases with increasing turbidity, it is reasonable to predict that fish will fail to assess the danger of predator presence in turbid water. Some studies have argued that fish are able to use turbid water as a shelter against predators (Abrahams & Kattenfeld 1997; Gregory, 1993; Gregory & Northcote, 1993) where reduced visibility lowers the predation risk (Gregory 1983). It would require empirical evidence to understand the role of algal turbidity on antipredator behaviour of visual foragers.

1.4 Turbidity-effects on prey selection

Natural selection leads us to expect that animals should make optimal decisions. An increase in the amount of prey potentially increases the amount of physical growth and reproduction in animals (Begon et al. 2006). However, animals might not always optimize feeding efficiency due to other contradictory demands, such as predation pressure, parental care or a degraded environment. A well-adapted animal might need to consider all options available before making a choice of what to do next. For that, some behavioural shifts occur. For example, brook trout (*Salvelinus fontinalis*) became more active and switched their foraging strategies from drift feeding to active searching in turbid water (Sweka & Hartman 2001). Many planktivorous fish select their prey individually (Brooks 1968). Prey selection is directly linked to feeding strategy and plays an important role in maximizing an individual's foraging success (Reiriz et al. 1998). When a predator has a choice of prey items that differ in profitability, the predator will most likely select the prey which ensures the maximum energy gain per unit time (Stephens & Krebs 1986). Several other hypotheses have been proposed to explain prey selection strategies. For instance, according to the prey-selection hypothesis, planktivorous fish should select the largest prey because energetically it is the best choice (Brooks & Dodson 1965). On the other hand, O´Brien et al. (1976) proposed "the apparent size hypothesis" according to which a planktivorous fish should choose the prey that appears largest in its visual field, irrespective of the item's absolute size. Reduced visibility due to elevated turbidity can pose a challenge on prey selection strategies of fish. Despite a number of recent studies, no firm suggestions have yet been proposed regarding prey selection strategies of fish in turbid conditions (Shoup & Wahl 2009, Helenius et al. 2013).

1.5 Turbidity-effects on social facilitation and distribution

Previous studies have shown that social foragers tend to prefer larger group sizes, because that provides a higher level of safety from predators (Krause et al. 1998), foraging efficiency (Clark & Mangel 1984), searching for mating partners (Hutter 2010), as well as quick and accurate decision making (Ward et al. 2011). In a variable environment where animals forage on patches of distributed resources, foragers need to gather information about the relative qualities of nearby patches before making a choice regarding where to forage (Giraldeau 1997). Social facilitation describes a situation when an individual in a group can monitor other group members and perform behavioural activities following conspecifics (reviewed by Galef et al. 1988). Thus, social foragers in larger groups have advantages through social facilitation that helps to improve their foraging decisions (Coolen et al. 2005).

It is important for individuals to track resources and optimally distribute themselves across available food resources. The ideal free distribution (IFD)

(Fretwell & Lucas 1970) provides a theoretical explanation for how animals might distribute themselves in an environment where the profitability of different food patches varies (reviewed by Milinski & Parker 1991). The IFD model has been used successfully in connection with optimal foraging theory (Ollason & Yearsley 2001; Ollason & Ren 2002). IFD assumes that all foragers are equal competitors, and everyone is free to enter each patch at any time and foragers have perfect knowledge regarding the profitability of the patches. However, in many subsequent studies several assumptions of this theory have been relaxed (Milinski 1988, Milinski & Parker 1991, Morris 2003). One might expect that turbidity affects social facilitation and distribution patterns of social organisms. These are, however, still not well-studied topics. As algal turbidity deteriorates the visual environment (Utne-Palm 2002), it is reasonable to assume that social facilitation among social foragers will become weaker in turbid conditions and turbidity will interrupt foragers' natural distribution pattern.

2. OBJECTIVES

I expect that as turbidity limits the amount and quality of information that fish can obtain about their environment, they should become less optimal in their behaviour. Behaviour is always a complex coordination of different activities. For example, while foraging, fish not only need to find food and make decisions about what prey to include in the diet, they also need to pay attention to predators or follow their conspecifics for optimal decision making. Previous studies have provided wide-ranging theoretical understanding about different foraging strategies of fish. In this thesis, I deal with selected aspects of the foraging and antipredator behaviour of three-spined sticklebacks (*Gasterosteus aculeatus*) that face sudden changes in their surrounding environment due to algal turbidity. I have divided the behavioural problems into several groups: antipredator response, habitat selection, prey consumption, diet selection, social interaction, distribution pattern etc. and conducted separate experiments for each subtopic. This work aimed to provide novel insight into how algal turbidity influences these behavioural responses.

The key questions in my thesis are:

1. How do algal turbidity and habitat complexity affect antipredator behaviour of three- spined sticklebacks? (Study **I**)
2. How does algal turbidity affect the risk assessment ability of three-spined sticklebacks? (Study **II**)
3. Are foraging success and prey selection affected by algal turbidity? (Study **III**)
4. How does algal turbidity affect the distribution of social foragers across food resources? (Study **IV**)

3. MATERIAL AND METHODS

3.1 Scope of the study

Study **I**: *Effects of turbidity and habitat complexity on antipredator behaviour of three-spined sticklebacks (Gasterosteus aculeatus)*

This study explored the interaction between algal turbidity and vegetation density in predator-prey relationship. The study was designed to examine the fine-scale (minute-by-minute) habitat choice of three-spined sticklebacks when confronted with turbidity, habitat complexity and the presence of a predator.

Study **II**: *Algal turbidity reduces risk assessment ability of the three-spined stickleback*

The objective of this study was to test how algal turbidity affects the ability of sticklebacks to detect predatory attacks by an avian predator when feeding, both alone and in groups.

Study **III**: *Effects of turbidity on prey choice of the three-spined stickleback (Gasterosteus aculeatus)*

This study focused on how different algal turbidity levels, prey densities, and prey size ratios (number of large to small prey) affect the foraging success and prey selection behaviour of sticklebacks.

Study **IV**: *Increased turbidity causes a mismatch between the distribution of social foragers and their resource*

This study examined whether algal turbidity affects the ability of social foragers to distribute themselves between two feeding stations in an ideal free manner and whether they can follow a change in food profitability between the feeding stations in both clear and turbid water.

3.2 Study species

The three-spined stickleback (*Gasterosteus aculeatus*) was chosen because it is well studied and, since the 1930s, has proven an excellent model species for behavioural studies (reviewed by Huntingford & Ruiz-Gomez 2009). Many behavioural aspects of this fish, such as foraging behaviour, habitat selection, group living, antipredator response etc. are well studied. As many aspect of experimental methodology and behavioural knowledge of sticklebacks have already been clarified, I had a very good starting point for my research questions.

Sticklebacks have a natural tendency to forage until near their satiation levels which is beneficial in experiments of feeding behaviour. Their populations are widely distributed in both fresh water and coastal regions of the northern hemisphere (Bell & Foster, 1994). They are frequently found in shallow coastal waters, which are affected by periodic algal turbidity. This means that sticklebacks regularly face the challenges of turbidity. I used wild-caught adult females (4.5- 6.0 cm in size) in all of my studies, because females are non-territorial and typically shoal during the summer (Wootton 1984). In addition, adult females are more responsive to predators than adult males (Giles & Huntingford 1984). Males often exhibit high levels of aggression and social dominance hierarchies when grouped together (Rowland 1984; Bakker 1986; McLennan & McPhail 1989).

3.3 Maintenance of study fish

All studies were conducted at two field stations: Husö Biological Station (60º17′ N, 19º50′ E) situated in the Åland Islands and Tvärminne Zoological Station (59º50′ N, 23º15′ E) located on the south coast of Finland. I seined sticklebacks from shallow beaches near the field stations and transported them to the laboratory within an hour. Before the experimental trials began, the sticklebacks were acclimatized in several glass tanks (80×40×30 cm) for 2-3 weeks. These tanks were connected with a continuous flow through a system of sea water (temperature 12-18ºC, salinity 5.20-5.45 psu). On average, 75 fish were kept per acclimatisation tank during this time and they were fed with frozen blood worms (*Chironomidae* spp), live *Mysis* spp. and water fleas (*Daphnia* spp.). During the pre-experimental acclimatisation period sticklebacks were also trained to perform experiment specific tasks. For study **II**, sticklebacks were trained to take red blood worms from a defined `food patch`. For study **IV**, they were trained to feed on *Daphnia* received through a continuous flow system. To increase the feeding motivation only hungry sticklebacks were used in studies **II**, **III** & **IV.** To ensure and standardize the hunger level I starved the fishes for 24h before the respective trials, following Peuhkuri (1998).

In study **I**, I used perch (*Perca fluviatilis*) as a fish predator. All perch were collected from adjacent bays of the research station by using gillnets. Perch are known as natural predators of sticklebacks (Wootton 1984, Reimchen 1994). As an avian predator, a model of a common tern (*Sterna hirundo*) was used (study **II**). Common terns are plunge divers that feed on various small fish, like sticklebacks in shallow waters. Water fleas (*Daphnia* spp) were used as a prey item of sticklebacks in study **III** & **IV**. Water fleas were collected from rock pools nearby the field stations. They are the stickleback´s natural prey and inconspicuous by being small and relatively transparent (Wootton 1976, Johnsen & Widder 1998).

3.4 Algal turbidity

For all studies I cultured unicellular (10-15 μm) planktonic algae (*Brachiomonas submarina*) to create the algal turbid water, following the procedure of Järvenpää & Lindström (2004). The initial culture was obtained from Tvärminne Zoological Station. Algae were grown in sea water (filtered through a 20μm sieve to eliminate possible grazers) in several white 60-litre buckets with continuous aeration under natural sunlight. I added a fertilizer containing nitrogen and phosphorus for quick growth. Turbidity levels were measured using a Hack 2100P turbidity meter and expressed in nephelometric turbidity units (NTU). This unit measures the angle of the light beam that is scattered back from the particles in the water column (Scheffer 1998) and is frequently used in behavioural studies to measure levels of turbidity (Carter 2009, Shoup & Wahl 2009; Helenius et al. 2013, Figueiredo et al. 2013). In all experiments, the range of turbidity levels varied between 2 and 20 NTU. This range is in accordance with previous behavioural studies (Abrahams & Kattenfeld 1997, Salonen et al. 2009, VanLandeghem et al. 2011). Turbidity levels were set manually before running each experiment by adding the initial culture to clear sea water.

3.5 Experimental set-ups and study design

A brief presentation of experimental designs used is given below. All study set-ups are described in detail in the respective studies **I- IV**.

3.5.1 General experimental set-ups

A combination of several approaches was used in order to answer the different research questions. Study **I** and the first experiment of study **III** were done at Husö Biological Station. Study **II**, **IV** and the second experiment of study **III** were carried out at Tvärminne Zoological Station. At Husö Biological Station, study **I** was conducted in an outdoor laboratory with a transparent roof and natural light levels, while study **III** was done inside a wet-laboratory under fluorescent light. At Tvärminne Zoological

Station, all studies (**II**, **III** & **IV)** were carried out in an outdoor laboratory (with transparent roof and walls) under ambient natural light. All studies were conducted during day time (10:00-16:00) and the water temperature during the experiments varied between 14 and 18ºC.

Before the actual trials, the experimental tanks were filled with either clear or turbid water in all experiments. In order to minimize potential learning and acclimatisation effects, all experimental fish were used only once and introduced to a randomly assigned experimental treatment. Experimental zones were shielded with black curtains to minimize disturbance and glare during experiments. After the trials, all fish were released in their respective natural habitat.

3.5.2 General study design

Study **I** was conducted in a square plastic aquarium (100×100×100 cm) and the bottom of the aquarium was divided into two halves. One half was treated as open habitat and the other half as a vegetated habitat (artificial sea-grass grid). In each trial, 20 female sticklebacks were released in either the vegetated or the open area and allowed to roam around the experimental tank for 10 min. Then one perch was released in the middle of the two halves by slowly lowering the perch into the trial area in a small container. This technique ensured that the experimenters did not disturb the natural activities of experimental sticklebacks during the predator introduction. The perch was then allowed to move around for another 10 min. The total experimental time was 20 min. Three different turbidity levels (low 2-3 NTU; medium 7-9 NTU; high 13-15 NTU) and three different shoot densities (100, 400 and 800 shoot/m^2) were used.

Study **II** was carried out in a square (100×100×30 cm) glass aquarium. One third of the experimental tank (30 cm width) contained artificial vegetation, called the sheltered zone. The rest remained without vegetation and was called the open area. A food patch was placed in the centre of the open area and a number of small stones were placed around the patch. The stones served as markers to measure the swimming distance of the stickleback. This study was conducted at two levels of turbidity; clear (<2±0.5 NTU) and turbid (12±0.5 NTU) with three group sizes (1, 3 and 6 fish). I released the fish, in the pre-assigned group size, carefully into the experimental tank using a fish net. When the fish aggregated around the food patch, a silhouette of a common tern (attached with transparent fishing line) was released to fly over the experimental tank. This set-up simulated a sudden predation threat from an avian predator. The immediate reaction of the experimental fish after the bird flight was the main observation of this study.

Study **III** was divided into two separate experiments following a similar experimental procedure but with different experimental designs. Two size groups of *Daphnia*, large (1.8-2 mm) and small (0.8-1 mm), were used in both experiments. In the first experiment (at Husö), single sticklebacks were offered *Daphnia* at three different ratios of large and small prey (large: small- 10:50, 20:50 and 50:50) at five turbidity levels (clear <1, 5, 10, 15 and 20 NTU). Similarly, in the second experiment (at Tvärminne) single sticklebacks were offered *Daphnia* at three size ratios (large: small 20:60, 40:40 and 60:20) at two turbidity levels (clear <1, 15 NTU). The duration of each test period was 5 minutes. In the first experiment, the study design gave an experimental matrix with three prey size ratios × five turbidity treatments. The second experiment corresponded to a factorial design with two water quality treatment levels (clear, turbid) and three prey size ratios.

Study **IV** used a rectangular glass tank (70×25×35 cm) in which a group of six sticklebacks was released to observe their distribution pattern between two adjacent food patches that differed in reward rates. For observational purposes, five vertical lines were drawn on the side of the tank to divide it into six equally wide compartments. *Daphnia* were supplied through a continuous flow system into the two opposite rear corners (called either high or low feeding station) maintaining two different reward ratios; 2:1 and 5:1. Two turbidity levels were used in this study: clear (<2±0.5 NTU) and turbid (14±0.5 NTU). The total length of the experimental period was 15 minutes which was further divided into three phases; 0-3 minutes, the no-food period when fish did not receive any food; 4-9 minutes, the first feeding period during which *Daphnia* was added according to predetermined ratios and 10-15 minutes, which was the second feeding period and the high and low reward sides was reversed.

3.6 Data collection

All trials of study **I**, **II** & **IV** were recorded by a Canon 3 CCD digital video recorder and later behavioural data were collected by watching the video tapes. In study **I**, I counted the number of sticklebacks in the open and sheltered habitat, as well as the location of the predator at 1 min intervals during each 20-min trial (10 min in absence/presence of predator). In study **II**, I recorded the experiment until 30 s after the tern silhouette had been released. During video analysis I recorded the position of each stickleback within 5s after flying the tern silhouette. In study **III**, the experimental fish was removed immediately after the trial and its total length was measured (to the nearest 0.1 cm) and also its wet mass weighted (±0.01g). After that the water of the experimental tank was filtered through a 0.5 mm sieve. I counted the number of large and small remaining *Daphnia* in the sieve. During the video analysis of study **IV**, I counted the number of sticklebacks in the six compartments of the experimental tank every 20 sec.

4. MAIN RESULTS AND DISCUSSION

4.1 Effects of turbidity on antipredator behaviour

In two studies I investigated the antipredator responses of three-spined sticklebacks in clear and turbid conditions. In study **I**, this was tested against piscivorous perch, while in study **II**, I used the sudden appearance of an avian predator (a silhouette of a common tern). The antipredator behaviour of the sticklebacks was indicated by increased dispersion rate and distance from the risky area, hiding under dense vegetation, increased use of the sheltered habitat and lower activity levels. It has been shown that a quick escape from the predation zone enhances the survival of an individual prey (Gilbert 1994). Studies **I** & **II** showed that after the introduction of the predator the sticklebacks showed stronger antipredator behaviour in clear than in turbid water. This included higher level of hiding in the shelter habitat (Figure 1, study **I**) or increased fleeing from the feeding zone (both distance fled and proportion of escaping fish) (Figure 2 study **II**). These results suggest that in turbid water sticklebacks might face more difficulties to show prompt antipredator behaviour responses against approaching predators. Therefore, the fish became less sensitive towards predator presence (Gregory 1993, Abrahams & Kattenfeld 1997). The ability to detect an approaching predator is a fundamental prerequisite for prey to avoid being captured (Brown & Chivers 2005). In the presence of a predator, fish usually move from open to more sheltered habitats (Werner et al. 1983, Gotceitas & Brown 1993) to avoid predation. Several studies have indicated that the foraging efficiency of predators is significantly reduced in densely vegetated aquatic habitats (Heck & Thoman 1981, Heck et al. 2003). But why did the sticklebacks show a weaker antipredator response in turbid condition? One possible explanation could be the limitations of visual perception in turbid water. In turbid water the shorter visual field possibly acts as a physical barrier to detecting the presence of predatory threats. It could also be possible that the sticklebacks felt safer in turbid water due to their perceived coverage (Gregory 1993) and therefore showed less antipredator responses. Previous studies have shown that turbidity can act as a shelter or cover for prey fish (Gregory 1993, De Roberties et al. 2006, Snickars et al. 2004). In study **I**, sticklebacks were sensitive to habitat availability and showed an affinity to structurally complex habitats over open space habitat both in the presence and in the absence of a predator. In the presence of the predator the increased use of sheltered habitat by the

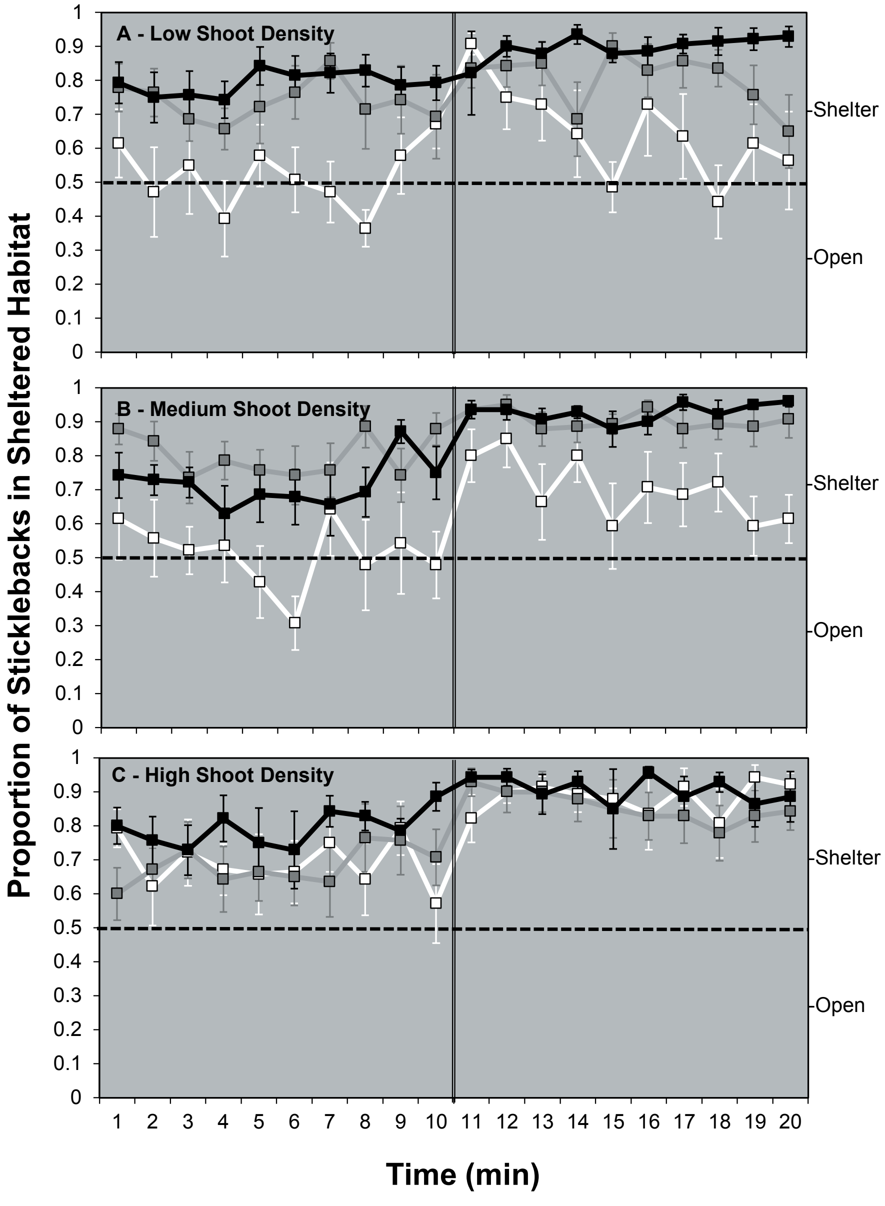

Figure 1: Proportion of sticklebacks in open water resp. sheltered vegetation habitats (mean ± 1SE) with different shoot densities: A) low, B) medium, and C) high. Turbidity levels are represented by colour gradation: low (open square, light grey line), medium (dark grey square/line) and high (black square/line).

sticklebacks could be considered as an antipredator strategy. There was a trend of increased use of sheltered habitat with increasing vegetation densities. It has been shown that three-spined sticklebacks can induce an antipredator response to an unseen predator only by following visual behavioural cues from conspecifics (Hogen & Laskowski 2013). As in study **II**, turbidity did not affect the tendency of the fish to flee to the sheltered habitat in study **I**. Instead the proportion of fish that escaped into the vegetated part of the experimental tank was a function of group size. This would suggest that stickleback were able to use visual cues in the turbid water. Therefore, I conclude that sticklebacks do not perceive turbidity as a cover from predators, and when possible, they utilized the available sheltered habitat to reduce further predation risk and social cues to assist them in finding a safer place.

Sticklebacks need to protect themselves from a wide range of predators. They use both structural and behavioural components for protection. Behavioural defence has two major components. The first one is the behavioural strategy which reduces the chances of being detected. The second one is the behaviour that reduces the chance of capture after detection by a predator. Previous studies have shown that prey animals, especially visual foragers, may cease their current activity and remain immobile when they are threatened by predators (Lima & Dill 1990, Smith 1992). In some cases, reduced activity levels or immobility may also be adopted by prey as a defence tactic to reduce the risk of being captured after they have been approached or attacked by a predator (Huntingford et al. 1994). According to the results from study **I**, sticklebacks reduced their overall activity levels after introduction of the perch predator in all combinations of turbidity levels and shoot densities. Besides this, sticklebacks restricted their foraging to complex habitat areas which is in line with Ibrahim and Huntingford (1989). Similarly, in study **II**, during the attack of the avian predator fewer sticklebacks escaped from the feeding zone and their average escape distance was also short in turbid water. Although the sticklebacks´ tendency to remain immobile in turbid conditions might be directly related to their vulnerability, it could also be considered as their behavioural defence strategy against an avian predator. Though I suspect that sticklebacks often failed to assess the possible risk of predation in turbid conditions, they eventually adopted the above mentioned behaviours that might reduce the encounter rate with a predator. There is evidence that sticklebacks can compensate for the reduction of visibility by increasing the use of non visual cues like olfactory cues for mate choice (Heuschele et al. 2009). However, there is no such evidence for antipredator behaviour. In the future, it will be interesting to study whether algal turbidity influences the use of complementary senses, such as visual and olfactory, in antipredator behaviour.

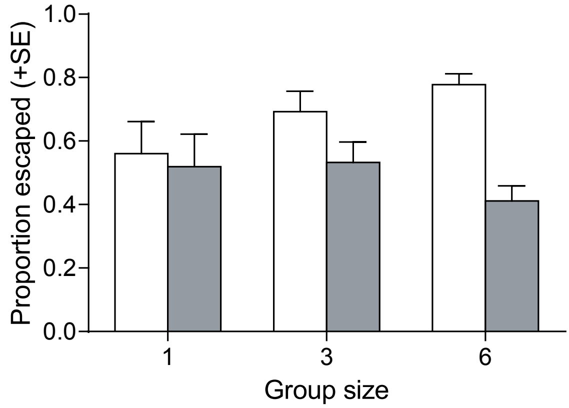

Figure 2: The proportion of sticklebacks escaping from a foraging patch after a simulated predator attack (a bird model flown over the experimental tank).

4.2 Effects of turbidity on prey consumption and selection

Foraging success depends on proper detection of prey, which largely depends on water clarity and light levels in the aquatic environment (Utne-Palm 1999). According to study **III**, the total prey consumption of sticklebacks was reduced at higher turbid conditions, which means that increased amounts of planktonic algae affected their performance negatively. This finding is in accordance with results from previous studies (Gregory & Northcote 1993, Wellington et al. 2010, Helenius et al. 2013). Sticklebacks feed only in light (Wotton 1984), which supports the conclusion that a reduced foraging success in turbid conditions was mainly due to a limitation of the visual field. A smaller visual field allowed the sticklebacks to detect relatively fewer prey items at higher turbidity than in clear water. In such situations, an increase in prey density could possibly compensate for the decreased reaction distance (Sweka & Hartman 2001). I provided prey (*Daphnia*) at three different densities, but no compensation effect was found on prey consumption. Instead, at all densities prey consumption remained at the same level. This suggests that the lower prey consumption at higher turbidity might not simply be a function of decreasing reaction distance. Previously it has been shown that the rate of prey encounter per unit time is a function of the predator´s visual field and prey densities (Holling 1959, 1966). Vinyard and O´Brien (1976) showed that increased turbidity causes a substantial reduction in the reactive distance that probably outweighs the importance of different prey densities in my experiments (Wellington et al. 2010).

In experiment 1 of study **III**, I found an overall positive relationship between prey consumption and body size. However, in experiment 2 of the same study I found this correlation only in clear water. It has been shown that in fish, visual acuity correlates positively with body size (Walton et al. 1994; Walton et a. 1992). It is possible that large individuals have better visual capacity than smaller individuals (Breck & Gitter 1983) and can detect prey from a greater distance. However, in turbid conditions, I did not observe such a correlation. It may be that body size and turbidity have independent effects on food consumption. Further investigation is needed for resolving this.

While foraging, prey selection is important to maximize the foraging success. When a fish predator has simultaneously located prey of different sizes, it should according to the size selection hypothesis prefer the larger ones, even if they are farther away (Brook & Dodson 1965). This prediction might be true in a clear aquatic environment, where a fish predator can locate the large prey from a reasonable distance. In this case, the fish will select the larger prey because it is possible that the greater energy return from it outweighs the time and energy spent swimming the longer distance. In my experiments (study **III**), sticklebacks followed the above prediction and showed a preference for large prey in clear water. However, at higher turbidity and when the ratio of large to small prey increased, sticklebacks became increasingly random in their prey selection (Figure 3; study **III**). This finding is in line with Helenius et al. (2013). But how does the prey selection strategy of sticklebacks change in turbid conditions? As mentioned earlier, increased turbidity possibly limits the field of view and reactive distance of sticklebacks. By reducing the reactive distance, turbidity also reduces the number of prey that can be attacked at the same time. As the field of view decreases with increasing turbidity, it is reasonable to assume that the number of visible large prey will also be limited. Sticklebacks preferably consume large prey within their field of view. In clear water with a larger visual field sticklebacks can prey solely on large Daphnia. However, with a limited visual field the number of large prey visible is reduced and the sticklebacks need to include small prey in their diet according to the ratio of large and small prey available. Therefore, I assume that sticklebacks have limited options to feed selectively at higher turbidity and turbidity causes them to switch to random feeding.

The effects of turbidity on prey selection by planktivorous fish like sticklebacks may have important implications for food web dynamics.

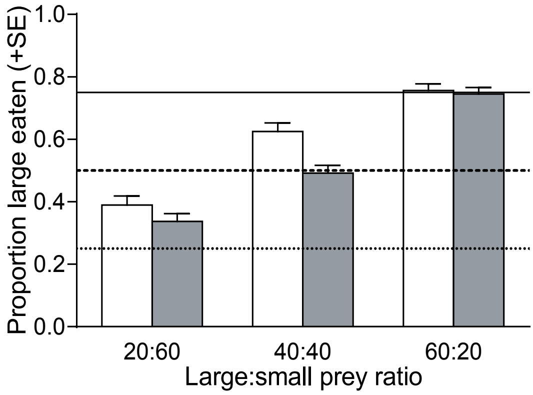

Figure 3: The proportion of large *Daphnia* included in the diet for study 2 done at Tvärminne. The horizontal lines indicate the expected proportion of large *Daphnia* included had the fish been feeding randomly. The dotted line is for the 20:60, hatched for the 40:40 and continuous for the 60:20 large to small prey ratio. The open bars are for clear water and grey bars for turbid water.

Many studies have shown that fish predators are selective for large (rich in energy) prey (Werner & Hall 1974; Myszkowski 1986). Similarly, I found that in clear water sticklebacks select larger *Daphnia*. In clear conditions, this process may result in the elimination of larger plankton and this may impose a strong structuring effect on the zooplankton community (Zaret 1980). My results suggest that turbidity may considerably weaken this effect.

4.3 Turbidity affects the distribution of group foragers

Food in nature might be distributed in patches (Iwasa et al. 1981). Often animals need to cross the empty space between the food patches to find better feeding areas. Within the experimental set-up of study **IV**, sticklebacks were initially able to track the food input rate at two feeding stations and their distribution approached the ideal free equilibrium state in both clear and turbid water. Similar findings were reported by Milinski (1979). However, when the positions of the high and low reward feeding stations were switched, sticklebacks took a longer time in turbid water to adjust to the new situation and approached the IFD equilibrium more slowly than in clear conditions. My results confirmed that turbidity interferes with the social foraging abilities of sticklebacks and that the fish faced difficulties to track the changes in the nearby patch qualities. Such difficulties may increase uncertainty regarding alternative feeding options. It is important for an individual to collect information about the available resources for potential foraging gain. Social foragers can access socially acquired information, known as public information, which helps them acquire knowledge regarding patch qualities (Galef & Giraldeau 2001). It has been shown that visual cues from feeding conspecifics play an important role in attracting other individuals to feeding areas (Pitcher & House 1987). But does turbidity interfere in transmitting social information among foragers? I hypothesise that, as turbidity has a negative effect on the use of visual cues (study **I**, **II**, **III**), low visibility at higher turbidity levels might also limit the transmission of social cues among social foragers. It may also be possible that sticklebacks modify their behaviour and make more conservative foraging decisions in new or unknown turbid environments. This, in turn, would result in a higher degree of aggregation in one place or slower movement between patches. Therefore, the above mentioned behavioural modification might cause sticklebacks' distribution pattern to deviate from the predictions of the IFD model. My results also highlight that aquatic organisms might be unaware of alternative food sources in turbid environments and, as a result, they will show a decreased foraging performance.

5. IMPLICATIONS OF THE RESULTS AND FUTURE STUDIES

From an evolutionary point of view, the three-spined stickleback is a highly adaptable species and has adjusted to a range of different environmental conditions (Schluter & McPhail 1992, Bell et al. 2004, Mckinnon et al. 2004). It is a debating issue whether the three-spined stickleback can be found in areas where the turbidity levels are usually high. Moyle (2002) claimed that it is unusual to find three-spined sticklebacks in turbid water due to their foraging nature, while according to Marshall and Elliott (1998), fish assemblies are not influenced by turbidity and sticklebacks can be found at higher turbidity (>25 NTU). The coastal area of the Baltic Sea, where I have conducted my studies, has become increasingly turbid during the last few decades (Sanden & Håkansson 1996, Bonsdorff et al. 2002). The stickleback is one of the most abundant fish species in the Baltic Sea (Jurvelius et al. 1996), and its populations are growing exponentially along coastal areas (Eriksson et al. 2009, Ljunggren et al. 2010). One possible reason for such population growth could be that populations of its natural predators, such as pike and perch, are decreasing in this area. Ljunggren et al. (2010) demonstrated that a recruitment failure caused the stock of pike and perch to decline in the Baltic Sea. Besides these, adjustment to turbidity could involve a switch to alternative behavioural strategies which may significantly increase the adaptive capabilities of sticklebacks in a changing environment. In my studies I have discussed several alternative behavioural responses that might outweigh the effects of algal turbidity. I did not study whether adjustment to turbidity also involved a switch to use alternative sensory cues, such as olfaction, but in the future it will be important to consider these options for a more comprehensive understanding.

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Turku, October 7th 2015,

Shakwat Sohel

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Shakwat Sohel

Effects of algal turbidity on foraging and antipredator behaviour

This thesis investigated how algal turbidity affects foraging and antipredator behaviour of fish. Due to anthropogenic nutrient loading, eutrophication causes algal turbidity in many coastal areas that notably degrades visual conditions. Therefore aquatic organisms often face the challenges of low visibility in turbid water. The results demonstrated that algal turbidity has overall negative effects on behavioural performance of fish, specifically foraging and antipredator behaviour of sticklebacks. The results also pointed out some alternative behavioural strategies of fish in turbid water that might help them to adjust to a changing environment.

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