

CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Tropical AgriSciences



Czech University of Life Sciences Prague

**Faculty of Tropical
AgriSciences**

**The role of personality in recognition of novel and
familiar chemical cues in the catfish *Silurus glanis***

DIPLOMA THESIS

Prague 2018

Chief supervisor: doc. Mgr. Ondřej Slavík, Ph.D.

Second (specialist) supervisor: Ing. Pavel Horký, Ph.D.

Author: Bc. Nikola Pfauserová

Declaration

I hereby declare that this thesis entitled “The role of personality in recognition of novel and familiar chemical cues in the catfish *Silurus glanis*” is my own work and all the sources have been quoted and acknowledged by means of complete references.

In Prague 27th of April 2018

.....

Nikola Pfauserová

Acknowledgements

I would express my sincere thanks to my supervisor doc. Mgr. Ondřej Slavík, Ph.D. for encouraging guidance, valuable assistance and inspiration. Thank Ing. Pavel Horký, Ph.D. for help with statistical analysis and experiment design. And last, but not the least, thank my family and friends for all the help and support.

Abstract

The olfaction plays a crucial role in social recognition of *Silurus glanis*. The influence of familiarity and pigmentation on preference to shoal with conspecifics was investigated. The literature review of this thesis focused mainly on – social recognition, familiarity, and albinism –and its consequences for aquaculture and fish welfare. The primary interest was paid to the role of olfaction in recognition of conspecifics in respect to fish welfare.

The experimental part provides new insights into social recognition of Wels catfish *Silurus glanis*. For the first time, we observed and demonstrated the ability of a catfish to make decisions based on olfaction only. A method that includes a binomial choice of familiar and unfamiliar chemical cues enabled the detection of social preferences of the individual. In the first part of the experiment, we observed a preference for familiar chemical cues in albino and pigmented juvenile *Silurus glanis* catfish. We found a significant preference for familiar cues in both groups (albino Adj P <0.0001; pigmented Adj P<0.0017). There were no differences observed in the ability of pigmented and albino individuals to detect chemical cues of conspecifics; the tendency to associate with conspecifics was also comparable. In the second part, we observed no preference of pigmented fish for unfamiliar albino chemical cues or an unfamiliar cues of pigmented fish. These results demonstrate that albinism may not affect fish olfaction and neither chemical cues of albino fish. Another observed phenomenon was lateralization; results revealed a strong preference for the left side of the arena when contained familiar chemical cues. We suggest further research to explain this phenomenon.

Key words: familiarity, group, behavioural syndrome, fish, catfish

Contents

1	Introduction and Literature Review	1
1.1	Introduction.....	1
1.2	Fish welfare.....	3
1.3	Social recognition	5
1.4	Living in groups.....	6
1.5	Familiarity	8
1.5.1	Physiological basis of familiarity.....	8
1.5.2	Preference based on kinship	11
1.5.3	Preference based on prior-association	12
1.5.4	Familiarity influenced by pigmentation	14
	Albinism.....	14
1.6	Laterality.....	16
1.7	Wels catfish <i>Silurus glanis</i>	19
1.7.1	General description and taxonomy	19
1.7.2	Biology and diet	20
1.7.3	Habitat and reproduction	21
1.7.4	Utilization.....	22
	Valued game fish.....	22
	Aquaculture.....	23
1.7.5	Aquaculture and the effect of familiarity phenomenon	26
2	Aims of the Thesis	27
3	Materials and methods	28
4	Results	37
5	Discussion	41
	Social recognition and preference to shoal with conspecifics	41
	The basis of recognition and discrimination of conspecifics.....	42
	Albinism and its consequences for aquaculture.....	44
	Laterality and fish behaviour	46
6	Conclusions	49
7	References	50

List of tables

Table 1. <i>Silurus glanis</i> production in past 10 years. Sum of “capture production” (CP) and “aquaculture production” (AP) together form “global production” (GP). AP specifically refers to output from aquaculture activities, which are designated for final harvest for consumption. Table contains data for world, Europe and Czech Republic areas (FAO 2018).	24
Table 2. Number of state events; i.e. the number of enters of fish to particular zone.....	37
Table 3. Time [s] spent in zones	37

List of figures

Figure 1. Production <i>S. glanis</i> in the Czech Republic in past two decades (1996-2015). Composition of global production – capture production (CP) and aquaculture production (AP) is represented by columns, the trend in percentage of aquaculture in total production is indicated by trend line. The line shows the percentage of aquaculture in global production. The global production (CP + AP) is increasing while the percentage contribution of aquaculture is decreasing (FAO 2018)....	25
Figure 2. Experimental design – illustrative figure. Experiment was composed of three parts; “ALBINO” and “BLACK” catfish were used as model animals; as treatment four types of water were used – with cues of familiar black group, with cues of albino group, with cues of unfamiliar black group, and clear water with no cues; binary choice was observed in each part.	29
Figure 3. Photo of the experimental tank (A) and schema of the tank (B). The tank is composed of reservoir tanks (N1 and N2) and arena (divided into “Lower” and “Upper” part and by longitudinal partition into Left and Right part). Reservoirs are equipped with taps; the arena is equipped with a drain. The grey dotted arrow shows the direction of water flow.	30
Figure 4. First part – testing of preference in black individuals. Choice of two types of water – “familiar” containing chemical cues of familiar group and “clear” tap water containing no chemical cues. In half of the trials, the fish (randomly selected half of the fish) were exposed to “familiar” water in the left side of arena (run out of the N1 reservoir tank, as you can see the picture), in half trials were sides switched and “familiar” water was present in right side of arena, N2 tank.	33

Figure 5. Second part – testing of preference in albino individuals. Choice of two types of water – “familiar” containing chemical cues of the familiar albino group and “clear” tap water containing no chemical cues. In half of the trials (randomly selected half of the fish) were fish exposed to “familiar” water in the left side of arena (run out of the N1 tank), in half trials were sides switched and “familiar” water was present in right side of arena – N2 tank (as you can see the picture). 34

Figure 6. Third part – testing of preference in black individuals. Choice of two types of water – “unfamiliar black” containing chemical cues of unfamiliar black group and “unfamiliar albino” water containing chemical cues of the unfamiliar albino group. In half of the trials (randomly selected half of the fish) were exposed to “unfamiliar black” water in the left side of the arena (run out of the N1 tank) and “unfamiliar albino” in the right side, N2 (as you can see on the picture). In half trials were sides switched and “unfamiliar black” water was present on the right side of the arena, N2 tank and “unfamiliar albino” water in the left, N1 reservoir tank. 35

Figure 7. Familiar vs clear; and unfamiliar pigmented vs unfamiliar albino preference. (A) Significant preference was observed in albino (Adj P <0.0001) and pigmented (Adj P <0.0017) individuals. (B) Weak preference (Adj P > 0.9589) was observed in “mixed” test, where a pigmented individual has chosen between two unfamiliar groups (pigmented and albino). 39

Figure 8. Time spent in the familiar zone. Effect of laterality on the choice of the familiar zone. Stronger (more significant) decision was observed in tests, wherein binomial choice only one option contained cues of conspecifics (A; B). When the tested animal had to choose between two unfamiliar groups, the side has no significant impact (C). 40

1 Introduction and Literature Review

1.1 Introduction

The diploma thesis is composed of literature review and experimental part, focused on fish behaviour and its possible consequences for aquaculture production. The first part is a review of social recognition and familiarity in fish, supplemented by a brief introduction to fish welfare.

Maybe because fish are so phylogenetically distant to humans in comparison with, e.g. mammals, we find it very difficult to empathise with them – we cannot hear them vocalise, and they lack recognisable facial expressions – these are primary cues for human empathy (Brown 2015). The topic of fish welfare is not so widespread and commonly discussed as the welfare of other animals. One part of animal welfare is to provide such conditions to allow the animal to express as much “natural behaviour” as possible. It can bring some constraints because fish are different from other vertebrates in ways that have significant implications for welfare and therefore it is almost impossible to specify conditions that guarantee the welfare in general, i.e. there are no universal conditions we should ensure to preserve fish welfare. We have to observe the natural behaviour, conditions and needs to be able to provide an adequate environment to fish under the human control, e.g. in aquaculture. There are even specific physiological and behavioural needs of a particular species, gender and age of fish and therefore we cannot guarantee the welfare by defining a simple set of husbandry conditions (FSBI 2002). Another approach is required for treatment of social-living species and species manifesting, e.g. strong aggression. At that point, the research of behaviour of animals could provide a useful tool for sustainable and welfare-friendly aquaculture management.

Many wild animals live in groups and are capable of recognising and subsequently prefer association with familiar individuals, i.e. those encountered in the past (Krause & Ruxton 2002; Muleta & Schausberger 2013). Social recognition and group forming have been documented throughout taxa and is known to be beneficial in many ways (Kohda et al. 2015; Ward & Webster 2016). Recognizing familiar from unfamiliar individuals has

an important implications for behavioural interactions among individuals and for social group formation, structure and dynamics (Ward & Hart 2003; Mateo 2004). Recent studies focused on fish behaviour revealed the fish prefer to shoal with familiars. These shoals are characterised by improved antipredator behaviour, stable dominance hierarchies and reduced aggression within a group (Barber & Ruxton 2000; Ward et al. 2003). The familiarity is reliant on individuals' abilities to recognise familiar individuals. The most discussed is recognition based on a combination of visual and olfactory stimuli (Ward & Hart 2003). In the natural conditions animals usually gather information based on a combination of stimuli to make a decision; in the laboratory conditions, we can observe the influence of each stimulus separately.

The experimental part is focused on the question how social recognition based on the olfactory stimulation is influenced by individual traits, e.g. albinism or lateralization. For the experiment purpose, juveniles *Silurus glanis* were used as a model species.

The Wels catfish *Silurus glanis* is known to its well-developed sense of taste and smell (Atema 1971). Therefore, we expect the olfactory cues will play the crucial role in decision making. The use of visual sense could be limited due to environmental conditions in which the catfish naturally occurs (Copp et al. 2009). In general, catfish as a large-bodied predator express great generalism and adaptability in its prey sources (Copp et al. 2009). As an apex predator, catfish has a high impact on other species and even on the whole food web and ecosystem (Vejřík et al. 2017). During last decades has been introduced out of its native range by a human (Copp et al. 2009) and nowadays the population of this so-called "megafish" seem to be at least stable. In contrast, most of the other large predators suffer because of loss of natural habitat, human influence, overexploitation, pollution, climate changes and others (Stone 2007). The great adaptability the catfish express is one of the main reasons why its invasion is so successful. The same feature, the adaptability, is highly valuable also in aquaculture. Therefore studies focused on a species behaviour can reveal such information which may be used to develop better utilisation techniques and technologies and improve the welfare in, e.g. intensive production.

1.2 Fish welfare

There are several concepts and views, how to define the welfare. Especially in case of fish welfare, it seems to be very difficult, to set a proper definition. We can distinguish three categories of welfare definitions. Feelings-based definition – composed in term of subjective mental state; the animal should feel well, being free from adverse experiences such as pain or fear, and having access to positive experiences, e.g. companionship in the case of social species. Function-based definitions – based on an ability of an animal to adapt to present environment. And nature-based – the animal can lead a natural life and express its natural behaviour; this approach requires the ability to compare how animals' behaviour differ in the wild and in captivity (Huntingford et al. 2006).

In general, the concept of “five freedoms” is perceived as a basis of animal welfare (FAWC 2009). Namely, freedom from hunger and thirst – to provide a nutritionally appropriate diet to avoid decreased welfare. Freedom from discomfort – appropriate water conditions should be provided (factors to be considered include levels of dissolved oxygen, pH, and ammonia; temperature; flow rates; and the presence of pollutants). Freedom from pain, injury, and disease – to limit disease outbreaks, and when the disease is found, it should be quickly diagnosed and treated; it is important to remember that poor health can be both a cause and a result of poor welfare (Ashley 2006). Freedom to express normal behaviour – appropriate densities and environmental conditions to enable the fish to exhibit natural behaviours should be maintained throughout the life cycle. Freedom from fear and distress – factors that cause fear, distress, discomfort, and other welfare impairing conditions should be minimised (Ashley 2006; HSUS 2008; FAWC 2009). We can abbreviate this as “good welfare means to be fit and feel good” (Webster 2005).

Threats to welfare can be divided into human-induced and natural threats, while both are partly overlapping and are closely related (Ashley 2006). Human activities, such as commercial fisheries, recreational angling, aquaculture, ornamental fish keeping,

anthropogenic changes to the environment and scientific research, are considered as a potential threat to fish welfare (Huntingford et al. 2006).

In commercial and sports fisheries (e.g. angling) we can meet issues such as tissue damage, physical exhaustion and oxygen deficit during capture, pain and stress during slaughter and pain and stress in tethered fish when live bait is used. The release of reared fish inappropriately equipped for survival in the wild or stocked fish introduced to lakes may deny the opportunity to migrate and may cause discomfort and death (FSBI 2002); inappropriate and unprofessional handling causes most of these problems.

In intensive production, the potential threats for fish welfare are high densities (in constraining conditions are closely linked to poor water quality), aggressive interactions (which can cause injuries and limited access to food) and diet deprivation. Even routine handling during husbandry procedures could cause stress to cultivated fish. Unnatural conditions such light-dark regimes, handling and constraint during transportation can lead to tainted conditions and consequently to easier transmission and spread of disease, even to wild stocks. Furthermore, crowding, handling and pain during slaughter may potentially compromise fish welfare (FSBI 2002).

As natural threats could be considered, e.g. predators, insufficient food availability and body condition, migration, parasites and diseases, suboptimal environmental conditions and conspecifics (Huntingford et al. 2006; FSBI 2002).

Many species are socially living organisms; they live in groups of the conspecifics, which provide some benefits, as discussed in the next section. The obligatory shoaling fish separated from the companions will tend to join a shoal. (Pitcher & Parrish 1993). Changes in group composition can lead to stressful situations by a novel hierarchy establishment (occurs during, e.g. artificial grading of fish groups), contact with unfamiliar individuals usually involve aggressive interactions which are connected to increased energy consumption and leads to stress and influence the welfare (Slavík et al. 2011). The primary costs are usually related to competition of conspecifics (or another species) over resources which may cause physical damage and depletion of energy supply (Beauchamp 2013). To have access to an adequate, nutritionally complete

diet is one of the fundamental requirements to ensure the fish welfare. We have to take into account the fact the fish vary greatly in their natural diet and way of feeding. They do not need to maintain constant body temperature, and in many cases, their requirements differ with the season and life history stage (FSBI 2002; Huntingford et al. 2006). One factor is usually linked to another and form complex conditions together (such as density influence disturbance and water quality and vice versa). It highlights the fact that, even for a particular species, we cannot guarantee the welfare by defining a simple set of husbandry conditions (i.e. requirements are different for gender or age groups within one species). This emphasises the need for sensitive on-the-spot indicators of welfare, i.e. generalisation is not possible (FSBI 2002).

Taking into account all this information, is important to monitor the nature of the behaviour in order to be able to ensure similar conditions in aquaculture. As we know, the composition of the group has a great influence on the level of stress and therefore also on the welfare of the fish.

1.3 Social recognition

The ability of animals to gather information about their social and physical environment is essential for their ecological function (Ward et al. 2004). The capability of fish to recognise familiar (or kin) individuals have a great impact on the understanding of interactions in this taxon. Social recognition and consequently the familiarity plays an important role in both, shoaling and territorial species. In shoaling species it affects, e.g. decision making; in territorial is known to reduce aggressive behaviour. In both, the familiarity highly affects a mate choice (Ward & Hart 2003).

Social recognition development is continuous throughout the lifespan. Templates for social recognition could be updated accordingly to environmental conditions and individual needs. Prior-association is used to learn familiar individuals – kin, neighbours, colony members, mates. Recognition and discrimination kin and non-kin individuals enable animals to allocate resources or evolve specific behaviour towards related conspecifics (Gerlach & Lysiak 2006). Social recognition is crucial in the differential

treatment of individuals in various social contexts as territory establishment and defence, in dominance hierarchies, reciprocal altruism, mate choice, parent-offspring interaction and nepotistic behaviour (Mateo 2004). Social recognition serves as an inbreeding-avoidance mechanism. Familiarity generates directed social learning – a fish learns more efficiently from familiar conspecifics. Familiarity could affect the transmission of foraging information in shoals, and therefore the social learning may play a role in shoaling preferences for familiar conspecifics (Swaney et al. 2001).

1.4 Living in groups

Life in a group can be described as a “ubiquitous phenomenon in the animal kingdom” (Krause & Ruxton 2002). Many wild animals live in groups and are capable of recognising and subsequently preferentially associate with those individuals, encountered in the past – familiar individuals. In nature, we can notice that animals often tend to form groups with kin or with familiar individuals (Muleta & Schausberger 2013). Forming groups and social cognitive abilities have been documented in many fish species; their cognitive abilities are comparable even to that in mammals or birds (Kohda et al. 2015).

The group living is known to be beneficial in many ways (Ward & Webster 2016). Shoaling or just joining a group provides anti-predator mechanisms, can increase predator detection, dilute the chance of capture and confuse the predators (e.g. Barber & Ruxton 2000; Griffiths et al. 2004; Jordan et al. 2010; Wolcott et al. 2017). Shoaling can enhance the food access and can lead to an increase in foraging success. Another benefit of shoaling is the higher chance to find a mate. Moreover, an increase in hydrodynamic efficiency is also one of the motives to be a member of a shoal (Krause & Ruxton 2002; Beauchamp 2013). Group living may also induce a ‘calming effect’ on individuals of gregarious fish species, manifested as a reduced metabolic demand, i.e. decrease metabolic rate (Nadler et al. 2016). Life in the group also brings some costs, often the degree of “disadvantage” grows along with the size of the group (Beauchamp 2013). We can name, e.g. limited resources and fight for them, as well as an increased risk of predation, increased possibility of the spread of disease and parasites, and so the possibility of infanticide (Krause & Ruxton 2002; Beauchamp 2013).

Recent studies have revealed, the fish showed preference to shoal with familiar conspecifics and join familiar groups (Jordan et al. 2010). The familiar groups have improved antipredator behaviour and set more stable hierarchies (Barber & Ruxton 2000; Jordan et al. 2010). More crucial role in antipredator behaviour the familiarity plays in predator avoidance than predator evasion (Wolcott et al. 2017), but still, the groups composed of familiar individuals benefit from faster predator evasion responses (Griffiths et al. 2004).

Most studies testing shoaling preferences were performed on small groups of individuals. There is a question if it takes longer to develop, or if is harder to achieve familiarity in groups where are more potential partners (Griffiths & Magurran 1997). According to Brown and Smith (1994), olfaction plays a major role in discrimination of familiar shoal-mates, i.e. fish could make their decision to associate, based on the odour of their habitual shoal-mates. And consequently, the recognition of familiar individuals does not necessarily need to be constrained by group size but is limited by odour presence.

The shoaling preference could change in time; it can shift e.g. with sexual maturity. In zebrafish, juveniles tend to spend more time with conspecifics – familiarity increases the preference. On the other hand, adult females prefer to shoal with unfamiliar, unrelated males (Gerlach & Lysiak 2006).

1.5 Familiarity

In natural conditions, social groups of animals are typically non-random associations of individuals. Such associations may be partly based on social familiarity among individuals, acquired through repeated past encounters and behavioural experiences among each other over some period of time. The factors that potentially affect the tendency to associate with familiar individuals remain poorly understood (Godin et al. 2003). There is even evidence of inter-species familiarity where preference to shoal with familiar heterospecifics was stronger than for unfamiliar conspecifics (Ward et al. 2003). The preference for familiars and their recognition is directly related to the social dynamics of the species. In shoaling species, the benefits of associating with familiars are likely to be more significant than in aggressive or solitary living species (Ward & Hart 2003).

1.5.1 Physiological basis of familiarity

All the senses as sight, hearing, touch, smell, taste or electroreception evolved to help animals to learn about the environment. The environment in which an individual exists shapes the senses (Brown 2015) and consequently the sensory abilities an animal has, each provides a particular type of information and plays a unique role in animal abilities to survive and thrive in the specific environment (Scowcroft et al. 2015). For example, chemical signals are long lasting, but they do not provide accurate directional information and work best at short distances between receiver and provider. Similarly, touch is useful when the animal is very close to a stimulus. Vision can give information about objects at greater distances, but it is very barrier dependent; in low light environments or at night, vision does not provide sufficient information. In contrast, sound provides animals with information about objects at great distances and in all directions. In other words, sound provides an animal with a three-dimensional “view” of its world, which is not hindered by currents, light levels, or even the presence of most objects (e.g. other organisms) in the environment (Scowcroft et al. 2015). In the natural conditions animals usually use the combination of all the senses to gather the complex information. In laboratory conditions, there is a possibility to observe the preference

and the decision making based on any sense individually. Still many of experiments are composed to observe preference based on a combination of stimuli – mostly the combination of the visual and olfactory stimulation (Ward & Hart 2003). The fact that animals can recognise and discriminate in favour of familiar conspecifics, is known in general. In previous experiments, it was often a preference based on multiple stimuli (e.g. Barber & Wright 2001; Ward et al. 2007; Griffiths & Magurran 1997; Slavík et al. 2011; 2012).

Visual Cues

Pigment pattern serves as a visual signal, and early experience with this signal variation determines future social behaviour. Individuals prefer to shoal with known, familiar, phenotype individuals even if it is not the self-matching phenotype (Engeszer et al. 2004). Fish can use visual cues to discriminate between potential shoalmates on the basis of body colouration when prefer to associate with individuals of similar appearance to themselves (McRobert & Bradner 1998).

There are several studies of familiarity based on visual stimuli. A link between familiar's recognition and personality was observed in European Sea Bass. The boldness was negatively correlated with time spent close to familiar conspecifics. The recognition was based only on the visual cues. Therefore, the European Sea Bass is able to recognise familiar only by the visual cue and behave according to its personality, i.e. shy individuals spent time near the familiar conspecifics (Benhaim et al. 2016). Waas and Colgan (1994) observed the ability to distinguish familiar and unfamiliar rivals on the visual basis alone. Male sticklebacks develop the ability in 4-6 days and do not require any other physical interaction with the conspecifics; and consequently, perform behaviour according to familiarity.

Acoustic Cues

Catfish, like other teleost fishes, evolved three major mechanisms to produce sounds. Namely stridulatory, swim bladder and hydrodynamic based sounds. First two are known to be used in communication (Fine & Ladich 2003).

Fish rely on sound production and hearing not only in terms of communication but also orientation or prey and predator detection (Maiditsch & Ladich 2014). A number of fish species use sounds as communication within social conspecifics, as predator defence, agonistic behaviour, in territorial defence and even in ritualized courtship behaviour. Several catfish species utilize the pectoral spine to produce stridulatory sounds, in certain groups of catfishes, the ability to produce sounds by contracting specialized sonic muscles exciting swim bladder evolved (Fine & Ladich 2003).

Chemical cues

Information about the social and physical environment is essential for animals to perform their ecological function. The information is a complex set of cues, where the odour cue is an important component of this information gathering across taxa. Chemical cues play an important role in facilitating fish social recognition (Ward et al. 2004) and are known to be important precursor for mate choice and reproduction and even spawning migration (Milinski et al. 2005; Miranda et al. 2005; Sorensen et al. 2005). Ensures predator-prey relationships (Brown et al. 1997; Jordão & Volpato 2000; Wisenden 2000; Mirza & Chivers 2001) and shoaling behaviour (Brown & Smith 1994; Engeszer et al. 2004; Behrmann-Godel et al. 2006). Taste and smell are important senses in fish as well as in other vertebrates. Catfish has well developed both – a sense of smell and taste, and is seriously dependent on these aptitudes (Atema 1971).

Catfish has a scale-less body covered with skin, and the taste buds are distributed all over the body surface. The density of taste buds is not uniform for all body parts. Barbells of catfish are densely covered by taste buds and therefore serve as “a set of external tongues” (Atema 1971).

Aquatic environment provides the ideal conditions for the solution and dispersing of chemical cues. The chemical information is used by aquatic organisms in decision making, crucial in behaviour. Chemical cues affect foraging, social recognition, reproduction or the assessment of predation risk (Wisenden 2000). Cichlids (family Cichlidae) are known to use chemical communication associated with many different

behaviours, e.g. parent-young interaction, kin recognition, reproduction, hierarchy formation or as alarm cues (Keller-Costa et al. 2015).

Recognition of conspecifics can be divided into two categories – direct and indirect. As indirect recognition of conspecifics, we can mark site-specific spatial recognition or the recognition where previous experience is not required. The differences are in the expression component, which animal provide (Mateo 2004). In such conditions where e.g. water is turbid, space is highly structured or at night, the chemical cues are expedient and advantageous. For species with a poorly developed visual sense the chemical communication is important (Wisenden 2000).

The African cichlid *Pelvicachromis taeniatus* can discriminate between its own, familiar and unfamiliar conspecifics odours (Thünken et al. 2009). According to laboratory studies, the cues are affected by habitat and fish is attracted by individuals that smell like themselves. In wild populations, where animals may move and forage freely, these cues would be temporally flexible and be spatial specific (Ward et al. 2004). Not only habitat but also diet composition form some specific chemical cues (Ward et al. 2004; 2005; Webster et al. 2007).

Fish can distinguish conspecifics from the same habitat as themselves and prefer association with them over individuals from different habitats. These preferences can update due to translocation to a different site – i.e. in wild population of three-spined sticklebacks *Gasterosteus aculeatus* the association preferences changed after short time of exposure to different habitat cues. The fish became familiar with cues of a new habitat after three hours (Ward et al. 2007).

1.5.2 Preference based on kinship

Hamilton (1964) in his inclusive fitness theory set the basis for kin selection and explain the altruistic behaviour among relatives. It is known as a cornerstone of behavioural biology and social evolution. For this theory a capability to the social (kin) recognition is crucial.

According to Tang-Martinez (2001), the basic mechanism of kin discrimination is “learning”, particularly associative learning and habituation. This mechanism could be denoted as a result of familiarity. We can discriminate the processes how animals distinguish kin from non-kin individuals, particularly the cues which animals use. All kin discrimination involves both, ‘recognition by association’ and ‘phenotype matching’ mechanisms. In vertebrates, it is the sensory capability, what determines the ability of an animal to distinguish between kin and non-kin, rather than the evolution of any specialized mechanism.

Mateo (2004) see several mechanisms of social recognition as a meaningful concept. He distinguishes four recognition mechanisms – the context-based mechanism; the mechanism based on recognition alleles; recognition based on prior association; and phenotype matching. All these mechanisms are proximately and functionally different and therefore should be distinguished. The recognition based on prior association (i.e. associative learning) is a widespread mechanism and is effective in a wide variety of situations. Advantageous is fact, that during the association the animal learn the cues or labels that identify the individual (familiarization). These cues are later recognized even out of the association context (Komdeur & Hatchwell 1999).

1.5.3 Preference based on prior-association

Prior association – familiarization – at first occurs during early development as siblings and parent recognition and later as discrimination between familiar and unfamiliar individuals (Mateo 2004).

Through a variety of diverse mechanisms, such as habituation, imprinting, associative learning, recognition of subtle behaviour, physiological and morphological cues recognition, familiarity may develop (Mateo 2004; Ward et al. 2004). Social recognition is a cognitive process where familiarity among conspecifics evolves. In other words, animals are able to remember and trait such individuals accordingly, based on previous interaction. The recognition is based on cues of individuals, inanimate objects or any proxies identifying the spatial location. Social recognition is beneficial or even required

in interactions such as kin selection, mating and mate choice, parental care, neighbour recognition, nepotism, avoidance or cooperation, and others (Mateo 2004).

The discrimination of visual or chemical cues (or its combination) is essential for familiars' recognition. Most studies were based on a combination of both (Ward & Hart 2003). Brown and Smith (1994) in a study on fathead minnows reported no preference for familiars based only on visual cues. However, the preference was expressed in only chemical cues expose and so, unsurprisingly, in a combination of visual and chemical cues. On the other hand, Engeszer et al. (2004) demonstrate that individuals of zebrafish discriminate only on visual cues basis. They make a decision based on pigment pattern and also on the early experience – therefore the familiarity determines shoaling preference.

Familiarity-based recognition takes some time to develop. In previous experiments, fish were kept together for long periods of time; i.e. Magurran et al. (1994) kept guppies for two months in one tank and then observed schooling preferences in familiar fish. Dugatkin and Wilson (1992) kept bluegill sunfish for more than three months in groups and observed their preference of association with familiar individuals. However, there is still a question, how long does it take to become familiar.

The amount of time needed to develop familiarity and how long it could persist, vary among species and ecological conditions (Ward & Hart 2003). Female guppies express a significant preference for school with their tank-mates after a period of 12 days. Females continued to school with tank mates for the duration of the experiment, 30 days in total. There is evidence that preferences can be maintained over long time periods (Griffiths & Magurran 1997). However, all these time periods seem to be at least species-specific. The preference of fathead minnows to shoal with familiar mates retain even after two months separation (Brown & Smith 1994). Utne-Palm and Hart (2000) observed decreasing aggressive behaviour within a pair of familiar juvenile sticklebacks sharing common food source after two and four-week periods and on the other hand increasing aggressiveness after two and four weeks of separation. The amount of time needed to become familiar and to “forget” is not uniform.

1.5.4 Familiarity influenced by pigmentation

As noted in chapter 1.4.1, the familiarity could be influenced by the behavioural type of individual. It is known, that behavioural types could be linked to pigmentation of animals. Therefore, the familiarity could be indirectly influenced by pigmentation.

Many animals use visual signals in communication; such signal could be, e.g. change in body colour. Particularly reptiles, amphibians, fish and cephalopods, have the ability to change their body colour. The main purpose of this ability could be thermoregulation, signalling and predator avoidance (Rodgers et al. 2013).

Because of lack of melanin pigmentation in albino individuals, this kind of communication is very limited. It leads to decreased ability of social interactions and kind of misunderstanding. The pale colour is linked to aggressive behaviour and cause more agonistic responses from other animals, while skin darkening signals the social subordination. Together with a combination of oddity and confusion effect, it could lead even to ostracism of albino individuals (Höglund et al. 2000; Slavík et al. 2016).

Albinism

Albinism can be simply described as “the result of homozygous recessive mutations from pigmented parents”. It is caused by the inherited absence of tyrosinase which leads to a lack of melanins in fish scales, skin and eyes (Cardem et al. 1998). Due to a mutation, an albino completely lacks the enzyme tyrosinase, needed in a chemical process that produces melanin pigments in vertebrates. The individual is completely colourless. The white, yellow, pinkish or even red colouration of some body parts is caused by the blood that can be seen through the colourless tissue of eye and skin. Tyrosinase does not influence the formation of carotenoids, and in an albino form of some species, these pigments remain present (van Grouw 2006). Not only the body colour and the red iris is caused by the mutation. Albinism also causes physiological and behavioural alternations (Slavík et al. 2016). In all animal species, the albino mutation is inherited through an autosomal recessive gene. The gene is not rare, occurs in most populations and albinos are born more frequently than one would expect. The reason why albinos are observed

so infrequently is related to their limited survival success. Due to the absence of pigments in the eye, albinos are very light-sensitive, and they have difficulties in observing depth. As a result of their colour and physiological constraints, they are easily detectable by predators (van Grouw 2006). The albino gene mutation seems to affect viability and fitness of fish; some sources see the mutation even as semi-lethal (Purdom 1992).

Albinism has been reported in numerous species, such as hagfish and lampreys, sharks and rays and numerous bony fishes, i.e. in grunts, or cyprinids. The presence of albinism in catfish was reviewed by Dingerkus et al. (1991). The albino catfish has been recorded in the wild (and reported in the literature) since the second half of 19th century (Dingerkus et al. 1991).

1.6 Laterality

The lateralization is defined as an asymmetrical specialization; i.e., one side is structurally different or perform different functions. We can distinguish the behavioural and physiological lateralization (Backström et al. 2015) and can observe it on the individual or population level. Most common example of lateralization is handedness in human, but in fact, many of animal species exhibit some kind of laterality (nonetheless substantial variability in the strength of lateralization exists within most species). The individual laterality means the individual manifests a lateralized behaviour, use one paired organ or prefer a particular direction repeatedly. This individual laterality may vary among individuals in the direction or the strength of preference. The laterality may be related to individual characteristics such as gender or personality (Reddon & Hurd 2008). Examples of “handedness” in some invertebrates and fishes is often a matter of anatomical asymmetry (Fine et al. 1996). Population laterality is defined as laterality when the same manner occurs in more than half of the individuals within a population. It means the evolutionary process has been at work and due to selective pressure for a particular side, the same threat evolved in more than fifty percent of individuals (Bisazza 1998). Population laterality can be explained mainly by internal factors as e.g. cerebral lateralization (Takeuchi et al. 2010). For example, the one side of the brain appears to be preferentially involved in recognition of conspecifics. It occurs in a wide range of species ranging from fish to humans (Bisazza & de Santi 2003).

There are many examples of lateralization in fish species. The first example of structural asymmetry is four-eyed fish *Anableps anableps* when the males gonopodium is right or left angled (Neville 1976). In order Phallostethiformes, males gonopodium has dextral and sinistral form, but females are bilaterally symmetrical (Breder & Rosen 1966). In the family Poeciliidae, the same asymmetries appear, some genera contain only sinistral species, one genus contains only dextral species, others are either sinistral, dextral, or symmetrical (Rosen & Bailey 1963). Another example of structural asymmetry is provided by flatfish where both eyes are located on one side of the head. The juvenile flatfish, the fry, undergo metamorphosis from the bilaterally symmetrical body, each eye on one side of the body, into both eyes on one side of the head in age ranging from

few weeks to months. The side where eyes are located is species dependent, only minority of individuals differ (Policansky 1982).

Usually, the physiological and behavioural laterality are connected. Takeuchi et al. (2010) reported the relationship between lateralized eye use during aggressive displays of male Siamese fighting fish *Betta splendens* and morphological asymmetry. The head incline would be associated with cerebral lateralization and individual laterality of behavioural responses. The preference for using the right eye when attacking a mirror image or a live rival (aggressive behaviour) was reported for several fish species. Thus, the direction of lateralization in fish appears to be opposite to that shown by all the other groups of vertebrates (Bisazza & de Santi 2003).

At the population level, lateralization of escape behaviour was demonstrated on a model species of poeciliid fish, *Girardinus falcatus*. The direction of turning during escape response evoked by a simulated predator, revealed a significant bias to escape rightwards in the first session. After several sessions, the preference reversed to escape leftwards (Cantalupo et al. 1995). The change in the direction of the escape was associated with a change in the behaviour of the fish after repeated testing. It could be a consequence of a learning phenomenon; this is not simple habituation to the stimulus but rather a development of the active strategy. This strategy occurred in both, mature and immature fish (Bisazza et al. 1998).

Catfishes first ray of the pectoral fin is minimally important for movement but is used to produce stridulatory sounds in several families of catfishes. In “handedness” analysis, most of the individuals showed bias to use right fin to produce the sound. Unlike examples of handedness in other invertebrates and fishes, this preference is not simply a matter of anatomical asymmetry but reflects a preference between two equally developed limbs (Fine et al. 1996). The presence of a population bias in lateralization may have some influence on social interactions and group structure (Bisazza et al. 1998).

There is evidence for a left-eye bias during scrutiny of conspecifics; the fish preferentially use the left eye in interaction with the familiar individual. During observing behaviour, left eye is used to monitor the familiar part of the environment,

while the right eye watches for potentially dangerous stimuli (Sovrano 2004). The left eye is used during mirror image inspection, the right eye in predator inspection (Santi et al. 2000). Social conflicts are usually solved by agonistic interactions where animals use cues to indicate dominance or subordination. A change in pigmentation is common for such signalling. The right body side signals usually express aggression and dominance whereas the left side signals the stress responsiveness and are connected to stress coping style (Backström et al. 2015).

The cerebral lateralization can play important role in cognitive function which likely have diverse fitness consequences (Bibost & Brown 2014). In the *Girardinus falcatus*, individuals selected for a high degree of lateralization performed better than those fish selected for reduced lateralization in several tasks – including schooling, foraging and spatial orientation (Dadda et al. 2007). The brain lateralization is associated with ability to separate different types of information into the two brain hemispheres, and thus enable separate and parallel processing (Rogers 2004). The advantage of laterality consists of possibility to divide an attention into several tasks. For instance, it may allow animals with a lateralized brain to cope with different tasks at the same time (Dadda et al. 2007).

There is an occasion to utilize the knowledge of lateralization to improve animal welfare. The idea to apply the knowledge of lateralization patterns could be exploited in farm management, e.g. during the handling of animals. Levels of fear and aggression could be reduced if the animal is handled from the correct side. The novel approach to human-animal contact may lead to improved welfare of animals. However, there is lack of practical implication in the field (Rogers 2011; Leliveld et al. 2013).

1.7 Wels catfish *Silurus glanis*

The European catfish has an elongated body with a broad head and wide mouth with three pairs of barbells, the longest on the upper lip. The anal fin is long; the dorsal fin is very short-based, adipose fin is absent (Maitland & Herdson 2009). Scale-less body is covered with skin, and the taste buds are distributed all over the body surface. Barbells serve as “a set of external tongues” thanks to the dense presence of taste buds (Atema 1971). *Silurus glanis* belongs to 20 largest freshwater fish species, is listed as 3rd world’s biggest fish, and the biggest European freshwater predator (Stone 2007).

1.7.1 General description and taxonomy

Common names: Wels; Wels catfish; European catfish; Sheatfish; Danube catfish (Velisek et al. 2007; Maitland & Lyle 1991).

Taxonomy formulated by ITIS (2018):

Class: Teleostei

Order: Siluriformes

Family: Siluridae Cuvier, 1816

Genus: *Silurus* Linnaeus, 1758

Species: *Silurus glanis* Linnaeus, 1758

The Siluridae family is only catfish family native to Europe. Most of the Siluridae species occurs throughout Asian continent and southeast Asia. Only two species of the family are native to Europe, *Silurus glanis* Linnaeus, 1758 and *Silurus aristotelis* Garman, 1890 endemic species to Europe (Bornbusch 1995). There is a possible hybridization of these two species (Paschos et al. 2004).

S. glanis has been widely introduced outside of its natural range and is present throughout most of Europe, nowadays considered as one of the worst alien species in this area. *Silurus aristotelis*, indigenous to Greece, is listed as strictly protected by the Bern Convention (Loannis et al. 2007). Catfish was intentionally, and often illegally, introduced mainly for the purpose of recreational fishing by local anglers (Freyhof & Brooks 2011) or aquaculture proposes (Copp et al. 2009). Another reason for introductions has been a biocontrol agent for regulating other fish numbers (Elvira &

Almodóvar 2005). The invasion success is driven by the omnivorous lifestyle of catfish. Recent studies have revealed that within-species variation in behaviour (i.e. animal personality) can affect the invasion process. The individuals' personality type may affect their colonization success, suggesting that some individuals might be better invaders than others (Cote et al. 2010). The potential impact in its introduced range includes disease transmission, hybridization (with *Silurus aristotelis*), predation on native species and possibly the modification of food web structure in some regions. However, *S. glanis* has also been in some countries reported to prey on other non-native species, which can be considered as a positive impact (Copp et al. 2009).

1.7.2 Biology and diet

Silurus glanis is freshwater fish well adapted to live in an environment with low visibility. The adaptation is possible also thanks to well-developed senses, namely taste (the taste organs are possessed e.g. on lips, barbells, skin and even fins; and are supplemented with large olfactory organs), sensitive electroreceptive system and sense of hearing. Unlike the highly developed sense of taste and smell, the sight is reduced. In consequence of all these adaptations catfish as an apex predator play a crucial role in ecosystem stability (Copp et al. 2009; Vejřík et al. 2017) and for a long time was considered to express a strong nocturnal feeding activity (Atema 1971). Recent studies revealed the catfish is not the strictly nocturnal predator but rather the opportunistic feeder. The catfish is active during the whole day, but the diel activity is influenced by season, i.e. temperature, stream flow and light intervals affects the activity during the year (Slavík et al. 2007; Vejřík et al. 2017). The diel dualism in energy consumption could be observed even at an individual level when some individuals express stronger night or day activity, some express no preference (Slavík & Horký 2012) and therefore the dualism could be interpreted as a result of different personalities, i.e. behavioural types. Certainly, the prey occurrence has a great impact on feeding style and activity. In some individuals, special strategies evolved, such as beaching behaviour when catfish capture (prey on) birds on land (Cucherousset et al. 2012). In captivity (controlled environment) populations show strongly nocturnal feeding activity (Boujard 1995).

As a predator feeding also at night, catfish can locate a piscine prey by accurate tracking its swim path in the absence of visible light. Catfish use olfactory and mechanosensory detection of hydrodynamical trace (Pohlmann et al. 2004) to localise moving prey. Chemical cues are detected by olfaction or by the extensive sense of taste which is used in localising non-moving food (Atema 1971). By the lateral line, a predator could detect hydrodynamical cues (Pohlmann et al. 2001). Thus, capture success of this slow predator benefits of searching and tracking prey in the dark when prey is visually less defended and approach from behind where all sensory systems of the prey (e.g. lateral line, olfaction) are less likely to detect the predator (Pohlmann et al. 2004).

Within the catfish population, we can find several dietary strategies: long-term generalists or specialists and also short-term specialization. It is probably a common feature of large-bodied apex predators in general and catfish as one of them has two typical features: enormous generalism (diet plasticity) and adaptability to new prey sources (Vejřík et al. 2017; Copp et al. 2009)

The diet of *S. glanis* is highly dependent on individual size (age) and is composed of plants, invertebrates (crustaceans, gastropods, insects) and vertebrates. In stomach content of bigger individuals were observed vertebrates such frogs, birds and rodents (Carol et al. 2009; Cucherousset et al. 2012; Czarnecki et al. 2003; Syväranta et al. 2010; Vejřík et al. 2017). Bigger individuals prey on smaller fish (Kottelat & Freyhof 2007); in some populations, the diet could be based on red swamp crayfish *Procambarus clarkii* (Girard, 1852) rather than fish (Carol et al. 2009). Larvae and juveniles are benthic and negatively phototactic. They feed on a wide variety of zooplankton, invertebrates and fish fry (Freyhof & Kottelat 2008).

1.7.3 Habitat and reproduction

S. glanis inhabits lower strata of large and medium-sized lowland rivers, backwaters and well-vegetated lakes. During the first year of life, juveniles shift to mid-channel habitats which serve as segregation between different age groups (Wolter & Bischoff 2001).

The males mature earlier than the females (Alp et al. 2004), approximately at the age of 2-3 years, with the weight of 1-2 kg. Spawning period range from April to June in middle Europe, in northern areas until August, with an average temperature around 20 °C. Catfish spawn in shallow, warm and well vegetated riverine habitats without current. Males defend small territories and build nests of plant material, dig shallow depressions or clean spawning substrate such as willow roots (Freyhof & Kottelat 2008). The eggs are laid in a large sticky pile by the female and guarded by the male until they hatch (Copp et al. 2009). Fecundity may vary according to environmental factors as water temperature or feeding and food abundance (Alp et al. 2004). Eggs hatch in 2-3 days and larvae stays in the nest until yolk sack is absorbed, usually another 2 to 4 days (Freyhof & Kottelat 2008).

1.7.4 Utilization

The traditional utilization of European catfish has a long history. The farm production started hundreds of years ago, and during last decades the catfish attract attention in modern angling society (Linhart et al. 2002).

Aquaculture comprises the diverse farming of aquatic organisms including fish, molluscs, crustaceans and aquatic plants. Farming requires some form of human intervention (such as regular stocking, feeding, protection from predators) to enhance production. Using the introduced (or alien) species have a significant socio-economic impact, therefore use local species is highly advisable. With the amount of food produced per hectare, the aquaculture production is considerably higher than, e.g. farming or livestock. Aquaculture can be a very productive way of use of resources. The fastest developing and expanding agricultural industries is aquafeed resources production (FAO 2018).

Valued game fish

The European catfish is a highly valued fish in Europe and has a very long tradition in European pond aquaculture, had been cultured extensively in temperate ponds for several centuries. In addition to its high-quality flesh, catfish was valued (and in

extensive pond aquaculture still is) as a “police” fish. They can utilise a low-value non-commercial fish (especially small cyprinids) and in that way, control their overpopulation (Proteau et al. 1996).

In open public waters, catfish are considered both as important predators providing biomanipulation service and as a highly-valued sport and trophy fish in recreational fishing (Randák et al. 2013). Some recent studies were focused on *S. glanis* production including economic point of view, chemical composition and sensory quality of meat, processing yields and traits or comparison of different ways of farming (Adamek 2015).

Aquaculture

Silurus glanis is produced predominantly in pond polyculture as a predator fish or open warm water systems. Less often is found in closed thermoregulated systems (Proteau et al. 1996). However, European catfish could also be produced in intensive aquaculture. Catfish is known for its high growth rate on a commercial diet, resistance to handling and relatively low water quality requirements (Szabó et al. 2015). The aquaculture of Siluroidei is not widespread in Europe; the production is significant only in a few countries: Germany, France, Italy, Belgium, Hungary, Czech Republic and the Netherlands (Proteau et al. 1996).

The possibility of using granulated feed in catfish cultivation makes the species suited for intensive pond cultivation. The polycultures cultivation seems to be more suitable in comparison with monoculture, where the fish reveals lower growth rate (Ulikowski et al. 2003). A significant sex effect occurs in catfish – growth and processing traits differ for males and females in the European catfish. Males express higher growth rate, are heavier and longer (Haffray et al. 1998).

We can divide Wels catfish production into the capture production and the aquaculture production. Currently, the global production is about 13,000 tonnes (Table 1). The production in the Czech Republic has increased steadily in past 20 years, from 1996 to 2015 from 64 to 189 t (Fig 1), with the aquaculture production ranging from 51 to 33 % during last two decades (FAO 2018).

Table 1. *Silurus glanis* production in past 10 years. Sum of “capture production” (CP) and “aquaculture production” (AP) together form “global production” (GP). AP specifically refers to output from aquaculture activities, which are designated for final harvest for consumption. Table contains data for world, Europe and Czech Republic areas (FAO 2018)

	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Capture production World	10223	11636	12289	16448	15654	11189	11741	10986	11142	11067
Capture production Europe	7011	8015	7517	12573	11902	7981	9118	8435	8745	8581
Capture production Czech Rep.	78	92	94	89	93	97	105	97	112	126
Aquaculture production World	1300	1749	1611	1530	1572	1327	1429	1782	1819	1814
Aquaculture production Europe	1214	1639	1472	1393	1420	1132	1231	1348	1407	1331
Aquaculture production Czech Rep.	49	63	60	58	47	49	52	61	54	63
Global production World	11523	13385	13900	17978	17226	12516	13170	12768	12961	12881
Global production Europe	8225	9654	8989	13966	13322	9113	10349	9783	10152	9912
Global production Czech Republic	127	155	154	147	140	146	157	158	166	189

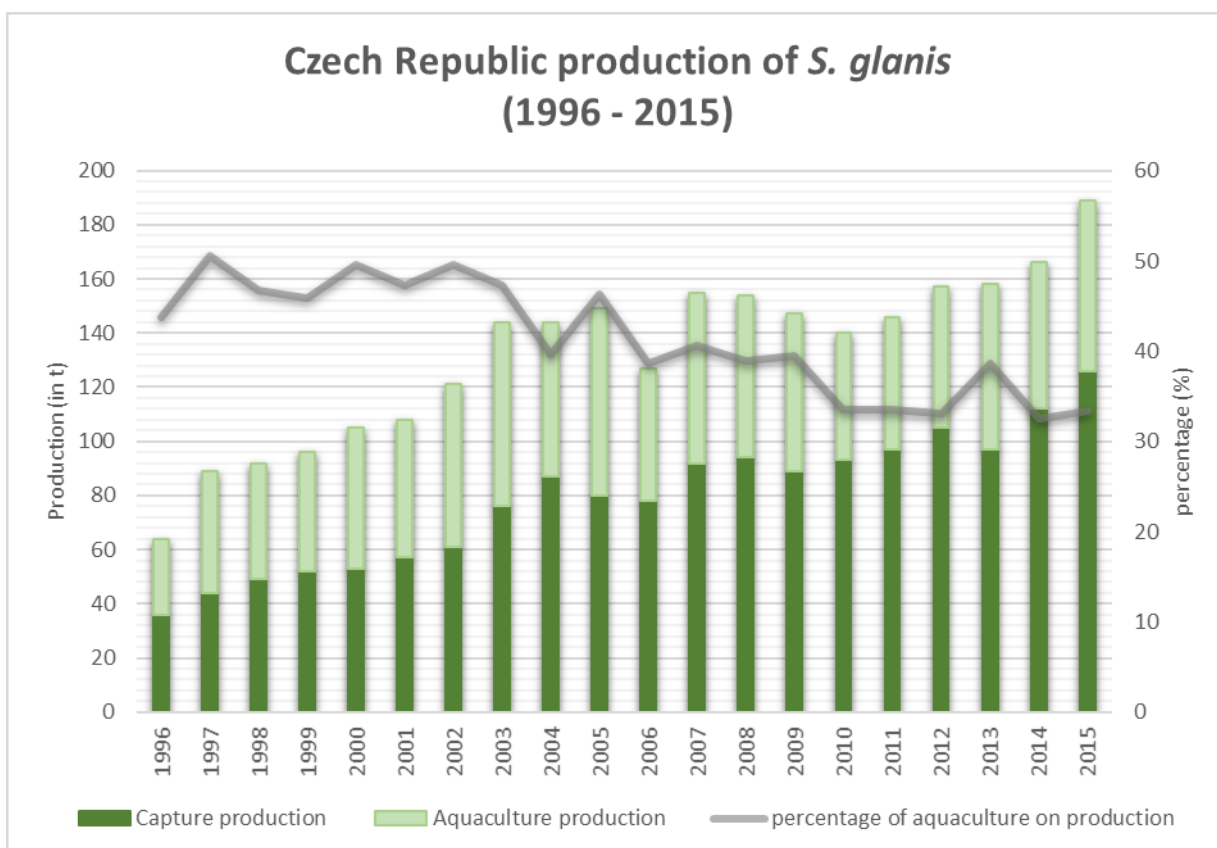


Figure 1. Production *S. glanis* in the Czech Republic in past two decades (1996-2015). Composition of global production – capture production (CP) and aquaculture production (AP) is represented by columns, the trend in percentage of aquaculture in total production is indicated by trend line. The line shows the percentage of aquaculture in global production. The global production (CP + AP) is increasing while the percentage contribution of aquaculture is decreasing (FAO 2018).

1.7.5 Aquaculture and the effect of familiarity phenomenon

The familiarity is beneficial in term of, e.g. better growth rate, body condition, survival of fish (Seppä et al. 2001) or improved foraging abilities (Swaney et al. 2001). Groups composed of familiar individuals are characterised by enhanced antipredator behaviour, increased shoal cohesion (Chivers et al. 1995) and stable dominance hierarchies (Höjesjö et al. 1998). Associating with familiars provide reduced aggressive interactions (Utne-Palm & Hart 2000) and is shown to promote social learning (Swaney et al. 2001). Shoaling with familiars reduce the risk of predation and therefore leads to lower investment in alarm behaviour, i.e. energy savings (Wisenden & Smith 1998). The energy investments and stress rates are lower during the interaction of familiar conspecifics in comparison to interactions between individuals without previous experience (Slavík et al. 2011).

Based on the knowledge obtained from the behavioural observations and experiments, the management of aquaculture can benefit from, e.g. change of the group composition management. The high stocking concentrations and grading of fish groups may affect the wellbeing and welfare. To minimise the impact of intensive aquaculture we have to understand the needs and use all the knowledge to supply the animals the best conditions. The quality of care and level of stress have a direct impact on the production.

2 Aims of the Thesis

The goal of this thesis was to explore shoaling preferences of catfish *Silurus glanis*, and investigate the effect of olfactory stimulation on decision making. Two different groups (albino × pigmented) were compared in respect to possible different social behaviour. A total of three treatments were carried out, involving binary choices of chemical stimuli of:

- i. familiar conspecifics × no cues in pigmented individuals;
- ii. familiar conspecifics × no cues in albino individuals;
- iii. non-familiar pigmented conspecifics × non-familiar heterospecifics (albinos) in pigmented individuals

We have developed following hypotheses:

- I. catfish follow chemical cues of familiar group, i.e. time spent in zones containing familiar cues is higher;
- II. the preference in albino individuals is lower than in pigmented individuals;
- III. the pigmented individual will spend more time in zones containing water with chemical cues of pigmented conspecifics;

In our experiment, we took into account the possibility that decision-making may be affected by laterality.

3 Materials and methods

The experiment was conducted at Czech University of Life Sciences in Prague laboratory in the period from 21st January to 20th February 2015.

The experiment was conducted in a special experimental tank and was composed of several parts. As model animals were used albino and pigmented individuals of *Silurus glanis* (Fig 1).

1. In the first part (Fig 3), we observed preference of pigmented individual based on the chemical stimuli. We observed a preference for the environment – water – without chemical cues (“clear”) and water containing chemical cues of the familiar group.
2. The second part (Fig 4) was similar to the first part but performed on albino individuals. As in the first part, we observed a preference between water with no chemical cues and water containing chemical cues of the familiar group.
3. In the third part of the experiment (Fig 5), we observed an individual preference of pigmented fish between water with chemical cues of a group of unfamiliar albino fish and a group of unfamiliar pigmented fish.

Preference was observed as the time spent in a particular part (zone) of the arena. We divided arena into four zones (Fig 2) – Upper left and Lower left, Upper right and Lower right. The left and right parts posed as “familiar” and “clear” zones (except third part, where posed as “albino” and “black” zone). In half of the trials, the left part contained familiar water, in the second half of trials the familiar water flowed through the right part of the arena. By switching of sides (left and right) we prevented the influence of preference of side over the familiarity and allowed us to observe laterality – if the individuals prefer one side more than the other side.



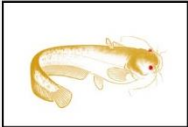



	Tested animal	Treatment
Part 1	<p>BLACK</p> 	<p>familiar × clear</p> 
Part 2	<p>ALBINO</p> 	<p>familiar × clear</p> 
Part 3	<p>BLACK</p> 	<p>unfamiliar BL × unfamiliar AL</p> 

Figure 2. Experimental design – illustrative figure. Experiment was composed of three parts; “ALBINO” and “BLACK” catfish were used as model animals; as treatment four types of water were used – with cues of familiar black group, with cues of albino group, with cues of unfamiliar black group, and clear water with no cues; binary choice was observed in each part.

Experimental tank (arena)

The experimental arena (Fig 2) dimensions were 240 cm length and 100 cm width; the water level was 15 cm. The arena was divided by adjustable partitions into several sections. Two separated reservoir tanks (N1, N2), each of capacity of 100 litres, were part of the experimental tank. The reservoir tanks were placed above the arena and provided with a tap. The tap ensured a constant and directed flow of water from the reservoir tank, through arena, into the drain. The drain was located on the opposite side of the arena – this composition created and ensured a moderate current during the trial. Dividing the arena by longitudinal partition prevented mixing of two types of water in the upper part and due to the artificial stream, the minimal mixture in the lower part. The movement of the fish in the arena was recorded by a video camera GoPro Hero 3, placed above the arena.

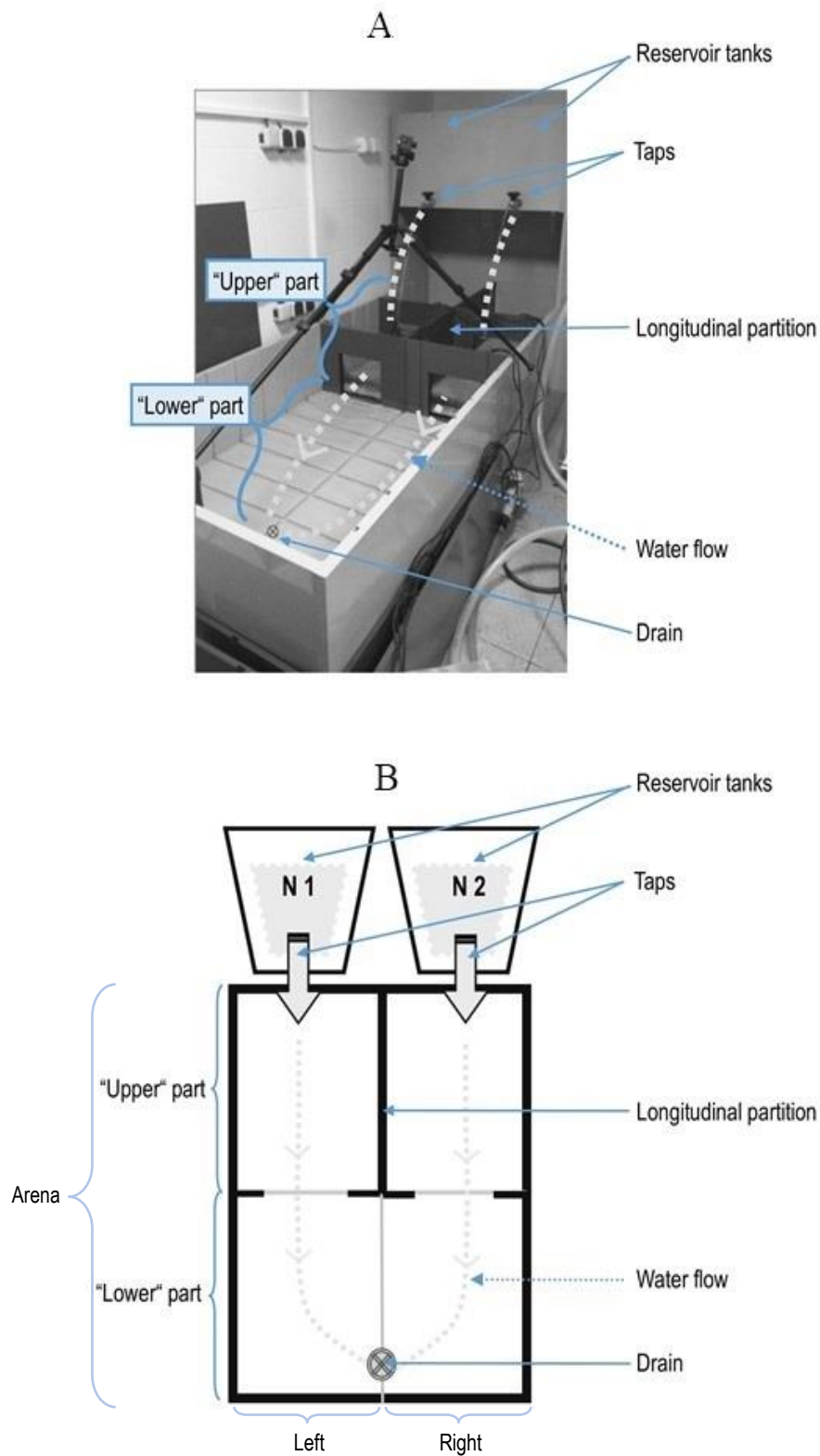


Figure 3. Photo of the experimental tank (A) and schema of the tank (B). The tank is composed of reservoir tanks (N1 and N2) and arena (divided into “Lower” and “Upper” part and by longitudinal partition into Left and Right part). Reservoirs are equipped with taps; the arena is equipped with a drain. The grey dotted arrow shows the direction of water flow.

Experimental animals

In the experiment were used 40 pigmented and 40 albino juvenile catfish *Silurus glanis*. Individuals were artificially bred and obtained from local fish suppliers. Catfish have been kept in “home” tanks (380 l) according to the colour (black, albino) for a period of 3 months. Five days before the start of the experiment, individuals were under general anaesthesia (2-phenoxyethanol, $0.2 \text{ ml} \times \text{l}^{-1}$) tagged with Passive Integrated Transponders with a unique code (hereinafter as “PIT”, e.g. Brännäs et al. 1994), weighted and measured. Using PITs have prevented re-using any fish repeatedly in the experiment (enabled us to determine individuals). During the experiment, catfish were six months old, the average weight of the pigmented individual was 13.4 g with an average length 111.5 mm; albino individuals weighted 13.5 g, body length 112 mm in average.

The home tank contained shelters made of plastic tubes (20 cm long, 6 cm diameter). Catfish were fed daily by granulated BioMar pelleted food (Biomar Group, Denmark, www.biomar.com). The light conditions followed the 12 hours (light and dark) cycle. Water purification was carried out using a biological filter in combination with UV sterilizer. The average water temperature was kept on mean temperature of 20 °C. Once a day the tank was manually cleaned of non-consumed feed and other solid residuals. Two-thirds of water was changed daily.

Experiment

Both reservoir tanks were filled with water, one with “clear” water and second with water from the home tank, where the group of 40 catfish was kept. The water was in the home tank for at least 24 hours prior to filling the reservoir tank (to be used as treatment). Filling the reservoir tank with the water containing chemical cues of the group was carried out by pumping through the aquarium filter. The arena was filled with clean water up to 15 cm level. Before the start of the trial, the drain outlet was opened, the camera was switched on, and both tanks’ taps were opened. As the beginning of a trial, we can mark the moment when the fish was released into the arena. The fish was released at the “lower part”, in the middle of the left and right zone, each individual in

the same place. The experiment was carried out on each fish once only. The content of the reservoir tanks was sufficient to run two trials. Due to the size of the aquarium (home tank), from which the water was pumped into the reservoir tank, it was possible to fill reservoir tank twice and therefore perform four trials (test four individuals) in one day.

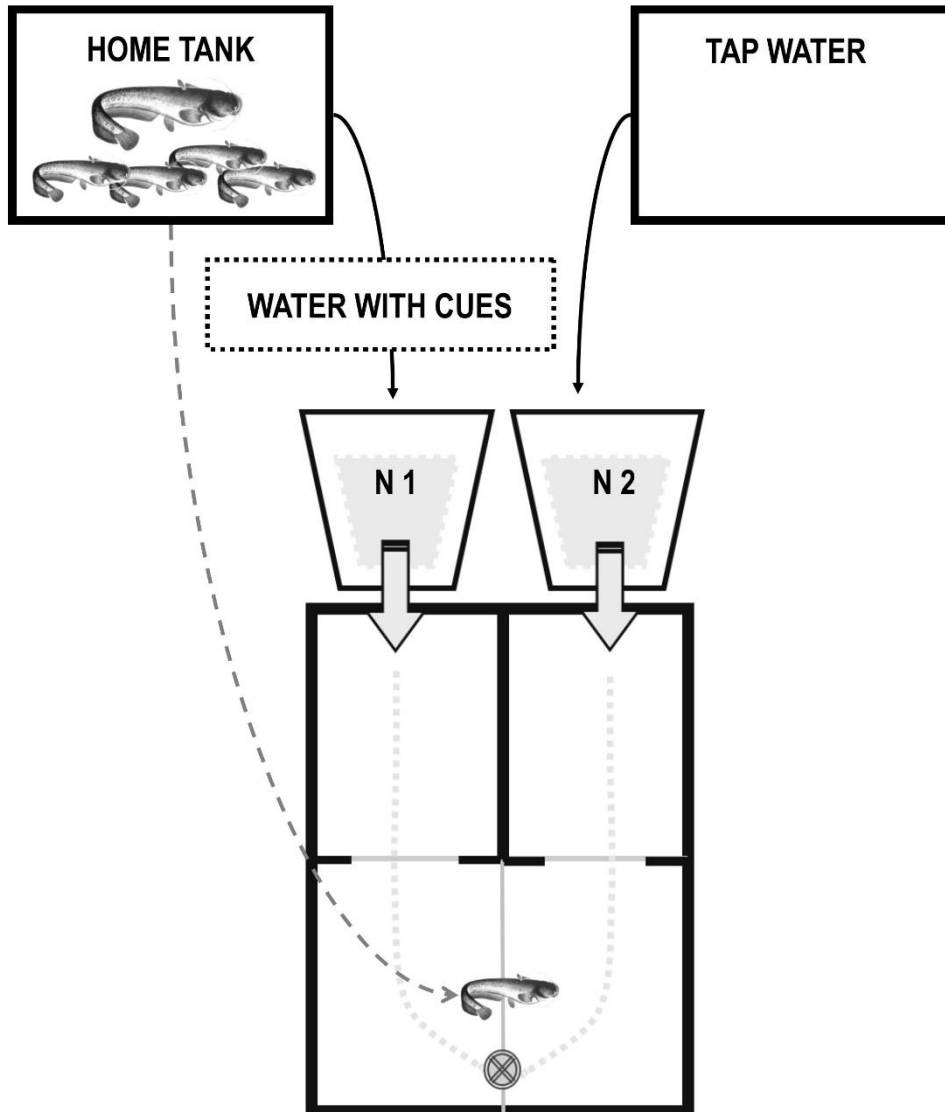


Figure 4. First part – testing of preference in black individuals. Choice of two types of water – “familiar” containing chemical cues of familiar group and “clear” tap water containing no chemical cues. In half of the trials, the fish (randomly selected half of the fish) were exposed to “familiar” water in the left side of arena (run out of the N1 reservoir tank, as you can see the picture), in half trials were sides switched and “familiar” water was present in right side of arena, N2 tank.

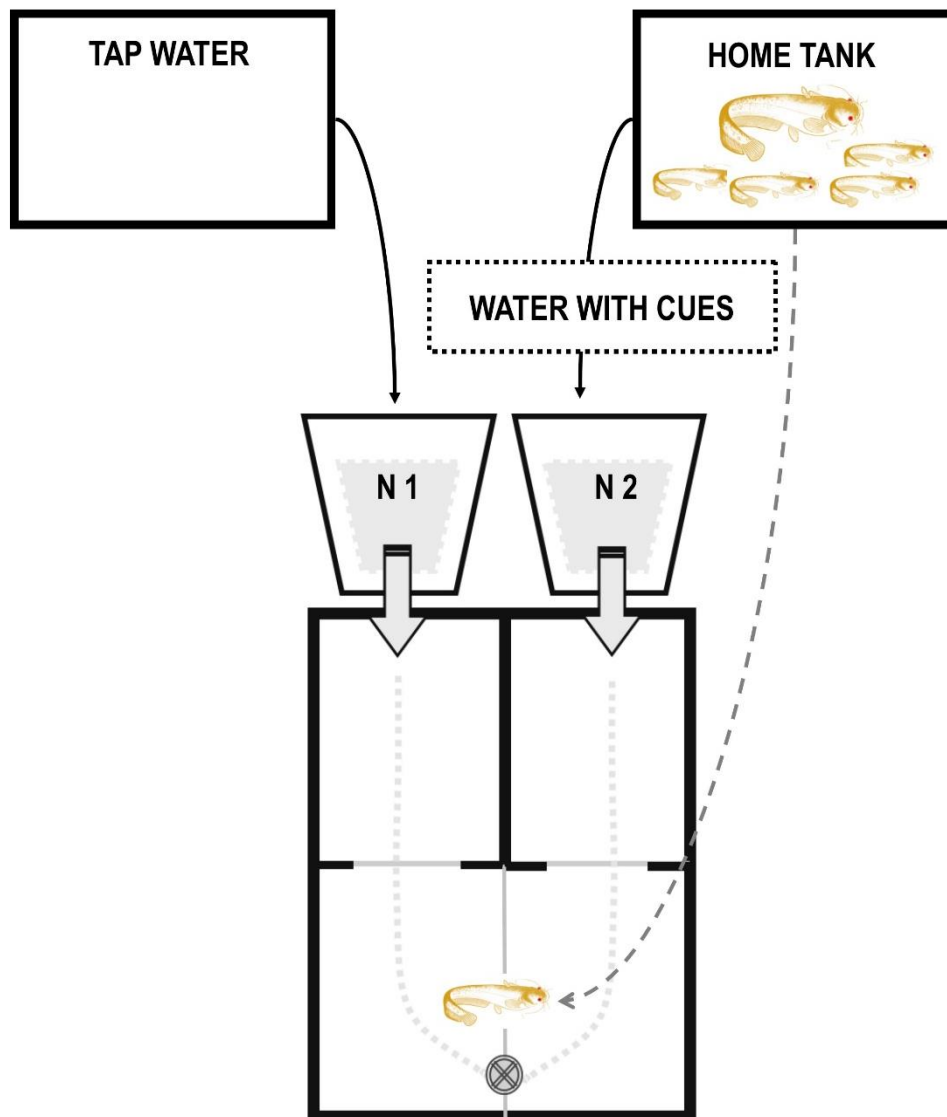


Figure 5. Second part – testing of preference in albino individuals. Choice of two types of water – “familiar” containing chemical cues of the familiar albino group and “clear” tap water containing no chemical cues. In half of the trials (randomly selected half of the fish) were fish exposed to “familiar” water in the left side of arena (run out of the N1 tank), in half trials were sides switched and “familiar” water was present in right side of arena – N2 tank (as you can see the picture).

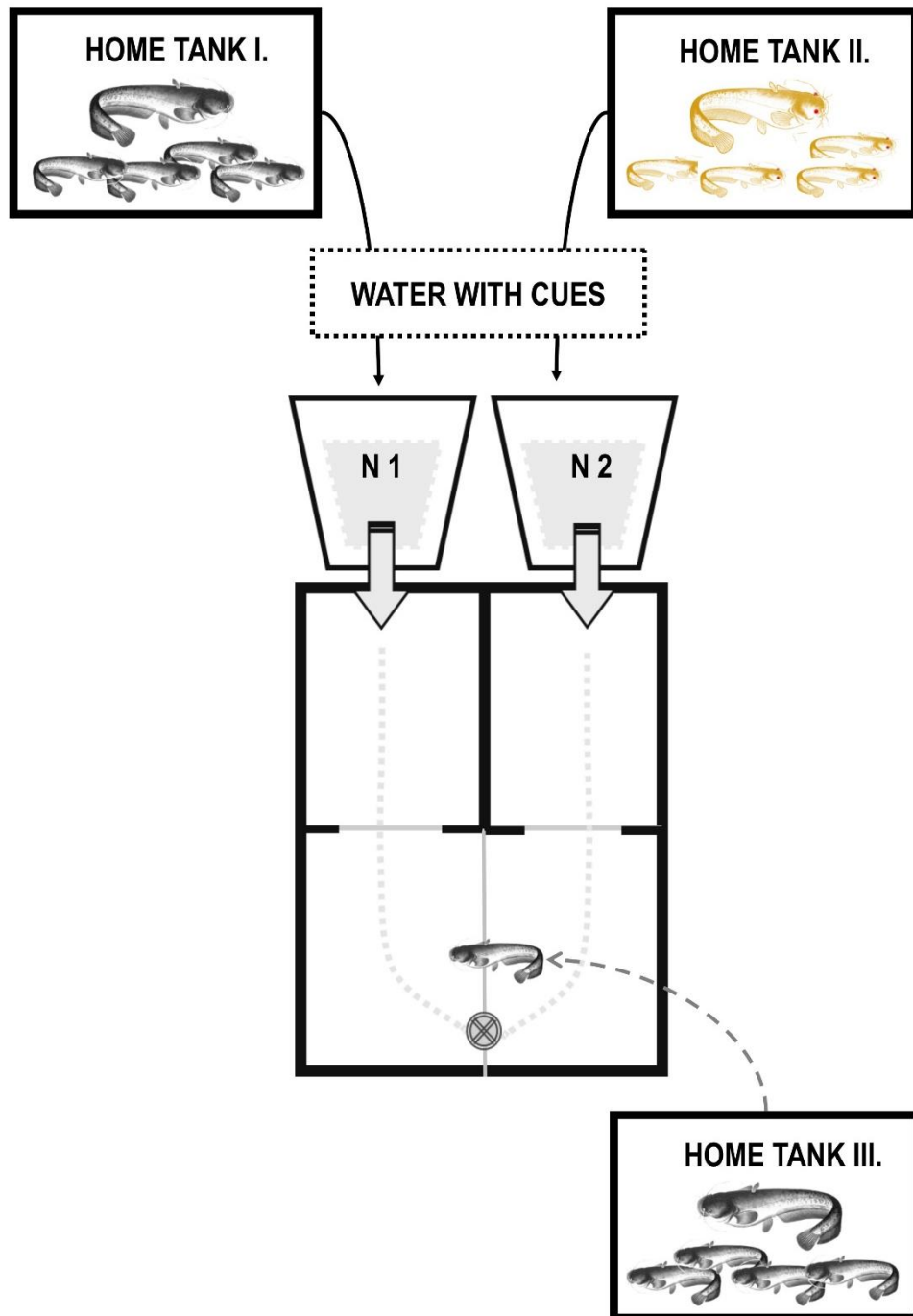


Figure 6. Third part – testing of preference in black individuals. Choice of two types of water – “unfamiliar black” containing chemical cues of unfamiliar black group and “unfamiliar albino” water containing chemical cues of the unfamiliar albino group. In half of the trials (randomly selected half of the fish) were exposed to “unfamiliar black” water in the left side of the arena (run out of the N1 tank) and “unfamiliar albino” in the right side, N2 (as you can see on the picture). In half trials were sides switched and “unfamiliar black” water was present on the right side of the arena, N2 tank and “unfamiliar albino” water in the left, N1 reservoir tank.

Data analysis

The experimental tank with an artificial stream made it possible to observe the individual preference between two types of water. In each trial, one fish was released into the arena for 15 minutes, individually. The time of presence of fish in each zone (e.g. familiar or clean) was observed, and movement of fish within the arena was recorded using a digital camera (GoPro Hero). During the trial, water was supplied from two separated reservoir tanks. Water was continuously flowing from taps towards the drain. Before each trial, the taps of reservoir tanks and the drain were opened, and moderate water current was reached. The own trial started when the fish entered the arena. We expect the Catfish make decisions based on chemical cues. Therefore we changed the water in the arena before the start of each trial to avoid any contamination from the previous trial. We cleaned and refilled the tank (arena) with tap water to the level of 15 cm.

To analyse the videos, we set 4 distinct zones and measured the time the fish spent in each zone. The analyse was made by BORIS (Behavioural Observation Research Interactive Software; Friard & Gamba 2016), setting four state events, one for each zone. In total 109 trials were analysed.

Statistical analysis

Statistical analyses were performed using the SAS software (Statistical Analyses System, version 9.4). The MIXED procedure was used to evaluate the time spent by an individual in the specified zone. This procedure allows modelling of a dependent variable with the inclusion of random factors (in our case the individual and the time of the experiment were chosen as a random factor). The differences between the classes were assessed using the so-called Tukey-Kramer test.

4 Results

During 109 trials we observed 2342 state events in total (for details see Table 2). We obtained data for 40 albino, and 39 pigmented individuals in familiar × clear treatment and 30 pigmented individuals in unfamiliar albino × pigmented treatment.

Table 2. Number of state events; i.e. the number of enters of fish to particular zone

Zone	albino (n=40)	pigmented (n=39)	mix (n=30)
Clear	421	370	320
Familiar	446	464	321
Left	431	452	336
Right	436	382	305

(n – number of tested individuals)

Table 3. Time [s] spent in zones

Zone	albino (n=40)	pigmented (n=39)	mix (n=30)
Clear	9,117.65	9,605.64	9,424.92
Familiar	14,888.84	13,717.25	8,589.83
Left	13,008.66	13,808.35	10,058.22
Right	10,997.83	9,514.54	7,956.53

(n – number of tested individuals)

Time spent in each zone was measured (Table 3). The results have shown that pigmented ($F_{5,542} = 8.70$, $P < 0.0001$; Figure 7 (A); Adj $P < 0.0017$) and albino catfish (Figure 7 (A); Adj $P < 0.0001$) preferred a water environment containing a chemical cue of familiar group (the water obtained from their home tank). On the contrary, the pigmented catfish from the so-called mix experiment has spent in both parts of the arena a comparable time (Figure 7 (B), Adj $P > 0.9589$). In other words, did not show the

preference for chemical cues of unfamiliar pigmented conspecifics or the unfamiliar albino individuals.

During the testing, it was shown that the preference of familiar water was also influenced by lateralization – whether water containing familiar cues flowed from the left or right tank ($F_{6,323} = 2.22$, $P < 0.0411$). If the familiar water flowed from the left, the albino individuals (Figure 8 (A); Adj $P < 0.0001$) and the pigmented (Figure 8 (B); Adj $P < 0.0089$) spent demonstrably longer periods of time. However, if the familiar water flowed from the right, in both groups, statistically detectable differences were not found between the use of the left and right side of the arena (pigmented catfish Adj $P > 0.9506$, albino catfish Adj $P > 0.6140$). It can, therefore, be assumed that the catfish preferred the left side of the arena. However, this fact was not proven in the so-called mixed test, in which the time spent in individual parts of the arena was comparable. No significant effect of lateralization was observed; whether the water of unfamiliar pigmented catfish flowed from the left reservoir tank and the water of unfamiliar albino individuals flowed from the right tank (Figure 8 (C), Adj $P > 0.9698$) or vice versa (Adj $P > 0.9999$).

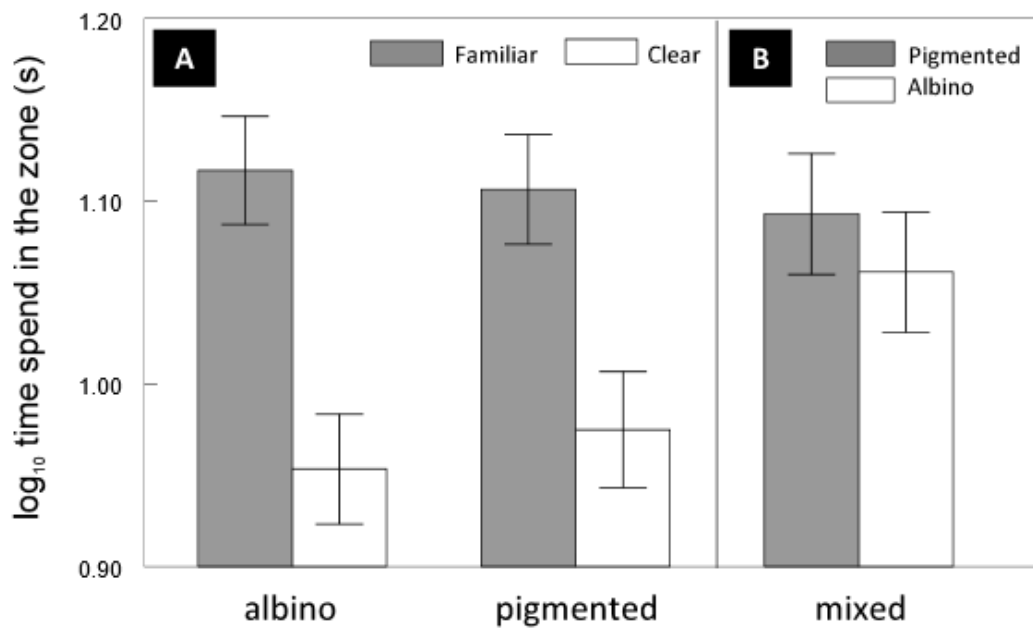


Figure 7. Familiar vs clear; and unfamiliar pigmented vs unfamiliar albino preference. (A) Significant preference was observed in albino (Adj P <0.0001) and pigmented (Adj P <0.0017) individuals. (B) Weak preference (Adj P > 0.9589) was observed in “mixed” test, where a pigmented individual has chosen between two unfamiliar groups (pigmented and albino).

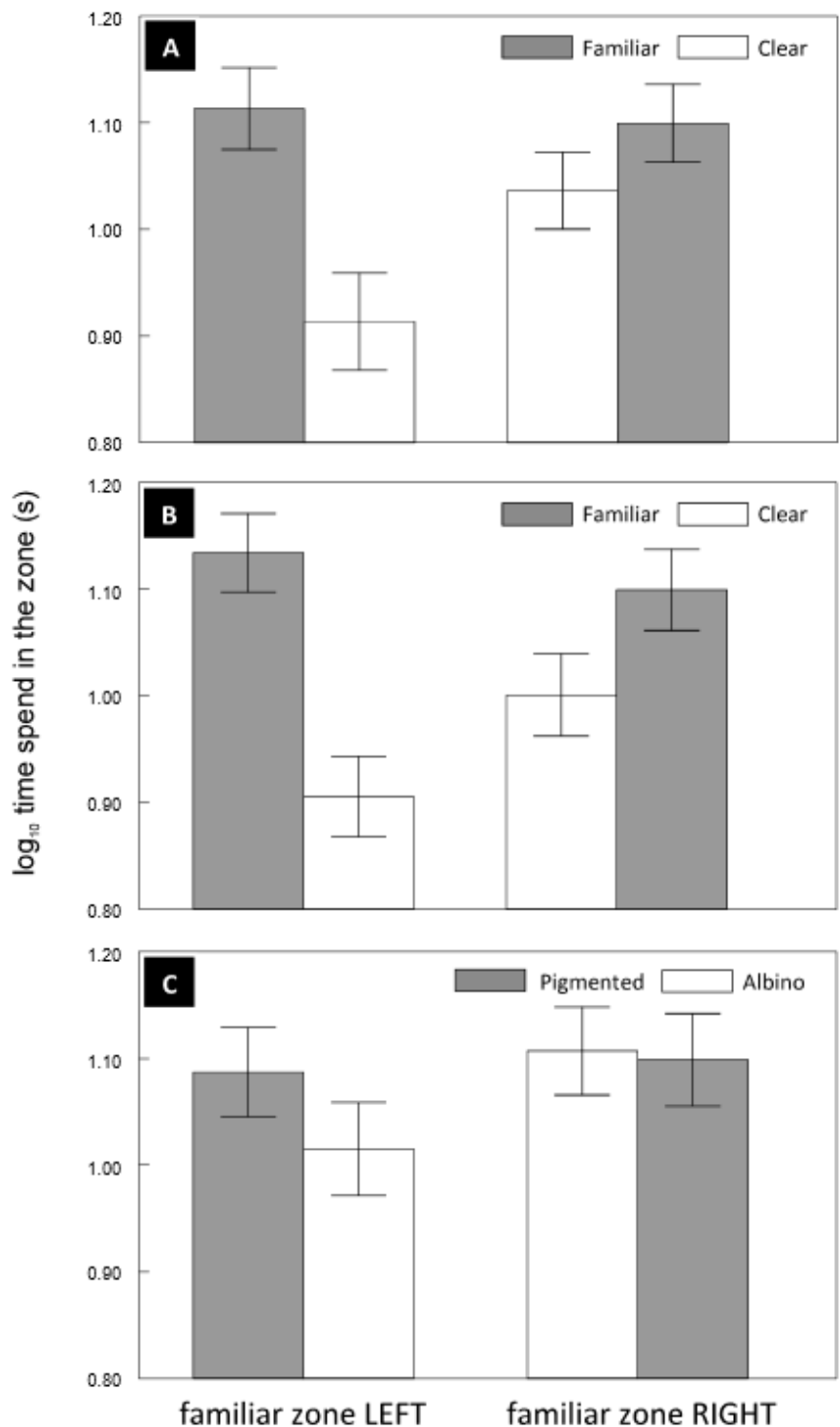


Figure 8. Time spent in the familiar zone. Effect of laterality on the choice of the familiar zone. Stronger (more significant) decision was observed in tests, wherein binomial choice only one option contained cues of conspecifics (A; B). When the tested animal had to choose between two unfamiliar groups, the side has no significant impact (C).

5 Discussion

Considerable attention has recently been paid to the topic of fish welfare. To be able to provide and consequently ensure the welfare of fish, the knowledge of suitable conditions (e.g. environmental, social) for the species is crucial. Understanding of animals' needs, in order to achieve high standards of animal production, is an issue for both, researchers and animal keepers.

In our research, we were focused on the social behaviour of Wels catfish and its aspects related to personal traits (predominantly albinism). As we expected, the results of preferential tests – shoaling behaviour, where individuals had a choice between water with chemical cues of conspecifics (familiar water) and water without cues, have shown that individuals prefer the familiar water. By this test, we have demonstrated the preference of catfish to associate, and the ability to follow the chemical cues of conspecifics, i.e. to decide on the basis of olfactory stimulation alone. We observed no differences in albino and pigmented individuals in the shoaling behaviour.

In the third part of our experiment, we were looking for the answer to the question “Does albinism smell?”. According to results, there is no significant preference for any of unfamiliar groups (albino × pigmented). That may suggest, there is no difference in chemical cues of albino and pigmented individuals. Further research is needed, to prove this suggestion.

Social recognition and preference to shoal with conspecifics

The evidence for fish to associate with familiars are usually shown in term of the benefits achieved. Associating with familiars may increase shoal cohesion, which can lead to improved antipredator behaviours and may thereby the lower risk of predation (Chivers et al. 1995). Afterwards, the reduced risk of predation is connected to the reduced investment of individual in alarm-substance cells production in fathead minnows *Pimephales promelas* (Wisenden & Smith 1998). It could be explained that familiar shoal-mates more rely on group-level antipredation responses whereas when in the context of unfamiliar shoal-mates, minnows increase their reliance on their own

ability to avoid predators (Wisenden 2000). Besides, brown trout *Salmo trutta* have revealed stabilised dominance hierarchies in groups composed of familiar members (Höjesjö et al. 1998) and reduced aggression was observed in the three-spined stickleback *Gasterosteus aculeatus* among familiar group members (Utne-Palm & Hart 2000). Furthermore, familiarity has been shown to promote social learning in the guppy *Poecilia reticulata*, when demonstrator – observer familiarity enhanced the rate at which guppies learned a foraging task (Swaney et al. 2001). Ward et al. (2003) presented evidence that familiarity preferences can even override natural preferences for conspecifics. Individual focal fish – chub *Leuciscus cephalus* preferred to shoal with familiar heterospecifics – minnows *Phoxinus phoxinus* over unfamiliar conspecifics.

Our results are consistent with recent findings. Based on mentioned scientific papers and our findings, fish preferentially associate with conspecifics and, in short, to shoal with familiars may be advantageous. However, since social recognition became a well-studied phenomenon, the way to recognise the familiars is still poorly understood and seem to be very diverse. In our experiment, we tested if familiars could be recognised on the basis of chemical cues.

The basis of recognition and discrimination of conspecifics

Animals usually use the combination of all the senses to gather the complex information about an environment; nonetheless, some are differently developed or useful in term of different tasks. Most of “shoaling” experiments are composed to observe preference based on a combination of stimuli – mostly the combination of the visual and olfactory stimulation (Ward & Hart 2003). In laboratory conditions, there is a possibility to observe the preference based on any sense individually. We tested the dependence of catfish on its olfaction with respect to social behaviour. Our results suggest the *Silurus glanis* may detect and subsequently associate with conspecifics on the basis of olfactory stimulation alone.

Brown and Smith (1994) have shown that fathead minnows are able to discriminate familiar from unfamiliar conspecifics based on a combination of visual and olfactory stimuli. When visual cues alone were presented, the data did not reveal a significant

preference. A strong preference was observed only when visual stimulation was present in combination with chemosensory cues. Ward et al. (2007) tested the influence of familiarity in three-spined sticklebacks and demonstrated that rather than familiarity (previous experience), the tendency to associate was induced by a self-referent chemical cue-matching instead the individual recognition by previous social experience. According to the results, habitat and diet-related cues plays a crucial role in social recognition. However, in contrast, there are still examples where, e.g. phenotype has been identified as a determining factor.

Another experiment based on visual cues showed zebrafish exhibit a strong preference for their own phenotype – wild-type or nacre. Thus, zebrafish were able to discriminate alternative pigment patterns visually, and there was a strong preference to shoal with individuals of the same phenotype expressed. However, if a tested individual was kept in a group of differently coloured individuals than itself, then preference switched to associate with individuals of the familiar phenotype. Therefore, results suggest the early environment plays a key role in the acquisition of intraspecific shoaling preference in zebrafish (Engeszer et al. 2004).

On the other hand, the oddity effect plays an important role in fish shoaling. Fish use visual cues to discriminate among potential shoal-mates and prefer to associate with individuals of similar appearance to themselves. The decision is based, e.g. on the size and colour (McRobert & Bradner 1998). The oddity effect allows a predator to overcome the confusion effect caused by a moving group of phenotypically similar individuals by selecting one that is distinct (“odd”) as a target. These mechanisms together lead to the formation of phenotype-assorted groups (Rodgers et al. 2013). Moreover, homogenous groups reveal better antipredator behaviour and less aggressive interactions (McRobert & Bradner 1998). The size of individuals is used as a criterion in the choice of shoaling companions; shoals are often size-assorted. Thus, predation risk is reduced by minimising phenotypic oddity, and the competition between size-classes may be potentially reduced too (Hoare et al. 2000). The ability of fish to make active association choices based on body colouration was demonstrated in mollies *Poecilia latipinna*. The experiment was based on visual stimulation, and strong preference to shoal with a group

of similar-coloured fish was shown (McRobert & Bradner 1998). Similar preference, colour matching shoal-mates, was observed in western rainbowfish *Melanotaenia australis* (Rodgers et al. 2010). The fighting fish *Betta splendens* females have been shown to preferentially associate with groups of individuals of similar colouration to their own. Moreover, they chose to swim near a group of similar fish rather than one individual – that suggests the shoaling decision is strongly affected by body colouration and by group size in *B. splendens* (Blakeslee et al. 2009).

Albinism and its consequences for aquaculture

The fish phenotype is another option to discriminate among potential shoal-mates. A distinct appearance may even cause opposite to shoaling – ostracism. Some differences in social behaviour of albino individuals were documented. In general, albinos are known to be less aggressive (Elipot et al. 2003; Slavík et al. 2016). In the experiment focused on the agonistic behaviour of pigmented and albino individuals Wels catfish, albinos exhibited less aggressive behaviour than pigmented fish. The lower level of aggressiveness was accompanied by maintaining longer distances among individuals. This phenomenon was explained as a lower inclination to shoal with conspecifics (Slavík et al. 2016).

Pigmentation plays a crucial role in communication and consequently social behaviour. Changes in fish colour can be divided into physiological – rapid response to environmental changes, and morphological – change in the morphology and density of chromatophores (Sugimoto 2002). The change in body colour can serve as, e.g. thermoregulation mechanism, communication and predator avoidance function. Many fish species can adapt by a change in body colouration as a response to a certain visual background; this may result in reduced predation risk (Rodgers et al. 2013). Consequently, animals preferentially select microhabitats and similarly coloured group mates, that enhance their crypsis and minimise additional costs connected with colour change (McRobert & Bradner 1998; Rodgers et al. 2010; 2013).

Communication accompanied by a change in individuals' colours is widespread in the animal kingdom. Visual signalling is used, e.g. during the competitive, aggressive and

sexual interactions of many animals. Fish use the body darkening to express submissiveness; subordinate brown trout signal defeat through a darkening and therefore reduce further attacks from dominant individuals. The darkening of subordinate salmonids is primarily a result of increased stress and acts secondarily in communication (Eaton & Sloman 2011). To express submission may lead to change in the behaviour of the opponent, and so minimise the potential risk of injury during fights in Atlantic salmon (O'Connor et al. 1999).

In an experiment of shoaling behaviour, albinos were ostracised by a group of pigmented individuals; this phenomenon might be caused as a consequence of the oddity effect, as mentioned above. Avoiding the albino individual may prevent distraction of uniform shoal (Slavík et al. 2015). Reduced shoaling preference in albino catfish was based on a combination of visual and olfactory stimulation (Slavík et al. 2016). In this sense, albinos are very disadvantaged in social communication based on visual stimuli. This disability can lead to significant problems in the context of integration into the group and consequently increased stress situations. Albinos cannot darken as pigmented individuals, and therefore a deteriorative social communication with other individuals is expected. The second aspect of darkening is, as mentioned above, matching with the environment. Even from this point of view, albinos are disadvantaged in comparison to pigmented individuals and increase the risk of predation in albinos may occur.

In the context of morphological and behavioural differences in albino and pigmented catfish, we tested the ability of pigmented catfish to recognise differently coloured (albino) individuals by olfactory cues alone. In this respect, we have demonstrated that the fish is not capable of distinguishing traces of albino and pigmented fish based on odour cues. Thus, the ostracising of the albino fish by the group of pigmented individuals, described by Slavík et al. (2015) is probably based on visual stimuli and can be considered as a consequence/expression of so-called "oddity effect" based on visual differences.

Slavík et al. (2015) suggest the ostracism is based on fear of visual oddity of albino individuals. Although the olfactory play an important role in social recognition in catfish, ostracism may be caused by visual cues only. Our data did not reveal a preference of pigmented catfish to shoal with unfamiliar albino or pigmented groups. We may expect the visual discrimination play a role in catfish social behaviour, because the ability to distinguish albino and pigmented fish by olfactory cues only, was not proven. For the further study, the question if albinism has any impact on individuals' chemical cues, remains to be explored.

Based on the information, that albinism is linked to less aggressive behaviour (Slavík et al. 2016; Elipot et al. 2003) but also reduced shoaling behaviour (Slavík et al. 2016), we would expect lower preference to shoal with conspecifics in albino individuals. This was not confirmed because they showed a similar tendency to associate, as same as pigmented individuals. Additionally, according to our results, we suggest albinism has no impact on chemical cues of catfish. The influence of pigmentation on social recognition and preference to shoal based on olfactory stimulation has not been confirmed.

Albinos have weakened sensory perception – vision (Allison et al. 2006), while the hearing is likely not affected by albinism in fishes (due to lack of melanin in the fish inner ear), as occurs in mammals (Lechner & Ladich 2011). Our results did not reveal any differences between pigmented and albino individuals in term of olfaction. On the other hand, the results indicate the catfish is not able to discriminate albino and pigmented groups only by chemical cues, i.e. there is no significant preference for any of two stimuli (albino vs pigmented fish cues).

Laterality and fish behaviour

Another observed phenomenon was lateralization. In our experiment, we noticed a pronounced preference for the left half of the arena, where both albino and pigmented individuals spent prolonged periods of time. The preference was even stronger when we take in count the familiarity.

Increased attention has recently been paid to the influence of lateralization on social behaviour in animals. As we know, behavioural and physiological lateralization can be distinguished (Backström et al. 2015). We can observe some consequences of cerebral lateralization in common behaviour (usually called “behavioural lateralization” or “laterality”) and hence, the behavioural lateralization, can be measured easily (Bisazza & Brown 2011).

One side of the brain appears to be preferentially involved in the visual recognition of conspecifics and social interactions (Bisazza & Santi 2003). The preference for using the right eye when attacking a mirror image or a live rival (aggressive behaviour) was reported for several fish species (Sovrano et al. 1999; Sovrano et al. 2001). There is evidence for a left-eye bias during an inspection of conspecifics, i.e. the fish preferentially use the left eye in interaction with the familiar individual. Similarly, during observing behaviour, the left eye is used to monitor the familiar part of the environment, while the right eye watches for potentially dangerous stimuli (Sovrano 2004). The left eye is used for the mirror image inspection, while the right eye in predator inspection (de Santi et al. 2000). The most frequently studied type of lateralization is the visual laterality. Due to laterally placed eyes in most fishes, the visual fields of eyes overlap only a little. By covering one eye or presenting a stimulus unilaterally, the differences in hemispheres function can be detected as differences in the behavioural response. The manipulation of fish can be non-invasive and therefore has a minimal effect on the welfare of tested animal (Bisazza & Brown 2011).

Laterality on a population level is likely to be beneficial in species living in groups, where, e.g. synchrony is vital. The strength of laterality seems to be heritable while the direction is environment and experience-dependent (Brown et al. 2007).

Olfaction is, in contrast to other senses (e.g. vision, hearing) “uncrossed” – i.e. input from each nostril is processed in the same half of brain (information from left nostril is processed in left hemisphere; right nostril, right hemisphere). The olfactory lateralization has shown in several mammals (including e.g. human, horse, dog), in birds and fish (Siniscalchi 2017). In chickens, the right nostril use is crucial during odours

imprinting and in familiar vs novel odour detection (Vallortigara & Andrew 1994); in pigeons is more important involvement of the right part of an olfactory system for spatial navigation (Gagliardo et al. 2011). Olfactory lateralization in fish was demonstrated in eels during migration to the spawning sites; individuals with blocked left nostril showed disturbed navigation, whereas no differences were reported in individuals using left nostril and controls (i.e. both nostril use) (Westin 1998). In other words, left nostril (and left part of the brain) is crucial in fish navigation; surprisingly, these results are opposite to those found in birds.

In our experiment, we observed a pronounced preference for the left half of the arena, where both albino and pigmented individuals spent prolonged periods of time. We cannot say whether this preference was driven by e.g. olfactory navigation; or affected by social or foraging behaviour (i.e. we cannot say for which purpose fish preferred the one side; if it was caused by e.g. searching for conspecifics or shelter). However, the left-side preference was related to presence of familiar cues. When the familiar zone was the right side of arena, the preference was not as clear as if familiar was the left side.

Understanding the links between personality (i.e. behavioural type; Sih et al. 2012) and familiarity can lead to better understanding of complex behavioural patterns. According to Benhaim et al. (2016), the link between familiarity and shyness is a general aspect of animal behaviour. The time spent near familiar conspecific is negatively correlated with boldness in European sea bass (Benhaïm et al. 2016). In the further study, I would like to investigate if there is any correlation between the behavioural type of individual (e.g. aggressive, bold) and the laterality.

6 Conclusions

The importance of understanding social behaviour, its causations and mechanisms to ensure good welfare of animals in aquaculture is crucial and recently discussed topic. The familiarity is known to be beneficial and advantageous in gregarious organisms. There are various ways how fish recognise familiar individuals. One of them is the olfaction. In our experiment, we were focused on social recognition of fish, based on olfactory stimulation. As a model animal, we used the Wels catfish. The aquaculture production of this species has increased during last decades distinctly. Nevertheless, their social behaviour is still poorly understood (though is known, e.g. the inappropriate group composition may cause stress and consequently affect the welfare).

According to our results, (1) the catfish can recognise chemical cues of conspecifics. (2) The capability of pigmented individuals to discriminate between pigmented and albino by olfactory stimulation was not proven, i.e. the effect of albinism on chemical cues of *S. glanis* was not detected. (3) Our results suggest a likely trade-off between familiarity and lateralization. However, further research should assess the influence of lateralization on the social behaviour of catfish.

We suggest the olfactory is crucial communication canal in *S. glanis* and consequently play an irreplaceable role in social behaviour. It would be beneficial to take this feature into account, with respect to utilization in aquaculture. The same approach would be expected in term of albinism and its consequences in catfish production and welfare. Applying the findings of fish social behaviour can be beneficial regarding aquaculture management in both – increased production and improved animal welfare.

7 Rerences

Adamek Z, Grecu I, Metaxa I, Sabarich L, Blancheton JP. 2015. Processing traits of European catfish (*Silurus glanis* Linnaeus, 1758) from outdoor flow-through and indoor recycling aquaculture units. *Journal of applied ichthyology* **31**: 38-44.

Allison WT, Hallows TE, Johnson T, Hawryshyn CW, Allen DM. 2006. Photic history modifies susceptibility to retinal damage in albino trout. *Visual neuroscience*, **23**: 25-34.

Alp A, Kara C, Büyükçapar HM. 2004. Reproductive biology in a native European catfish, *Silurus glanis* L., 1758, population in Menzelet Reservoir. *Turkish Journal of Veterinary and Animal Sciences* **28**: 613-622.

Ashley PJ. 2007. Fish welfare: current issues in aquaculture. *Applied Animal Behaviour Science* **104**: 199-235.

Atema J. 1971 Structures and functions of the sense of taste in the catfish (*Ictalurus natalis*). *Brain, Behavior and Evolution* **4**: 273-294.

Backström T, Heynen M, Brännäs E, Nilsson J, Magnhagen C. 2015. Dominance and stress signalling of carotenoid pigmentation in Arctic charr (*Salvelinus alpinus*): Lateralization effects?. *Physiology & behaviour* **138**: 52-57.

Barber I, Ruxton GD. 2000. The importance of stable schooling: do familiar sticklebacks stick together?. *Proceedings of the Royal Society of London B: Biological Sciences* **267**: 151-155.

Barber I, Wright, HA. 2001. How strong are familiarity preferences in shoaling fish?. *Animal Behaviour*, **61**: 975-979.

Beauchamp G. 2013. *Social predation: how group living benefits predators and prey*. Elsevier. ISBN 0124076548 **336**.

- Behrmann-Godel J, Gerlach G, Eckmann R. 2006. Kin and population recognition in sympatric Lake Constance perch (*Perca fluviatilis* L.): can assortative shoaling drive population divergence?. *Behavioral Ecology and Sociobiology* **59**: 461-468.
- Benhaïm D, Ferrari S, Chatain B, Bégout ML. 2016. The shy prefer familiar congeners. *Behavioural processes*, **126**: 113-120.
- Bibost AL, Brown C. 2014. Laterality influences cognitive performance in rainbowfish *Melanotaenia duboulayi*. *Animal cognition*, **17**: 1045-1051.
- Bisazza A, Brown C. 2011. Lateralization of cognitive functions in fish. *Fish cognition and behavior* 298-324.
- Bisazza A, Rogers LJ, Vallortigara G. 1998. The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neuroscience & Biobehavioral Reviews* **22**: 411-426.
- Bisazza A, de Santi A. 2003. Lateralization of aggression in fish. *Behavioural brain research* **141**: 131-136.
- Blakeslee C, McRobert SP, Brown AC, Clotfelter ED. 2009. The effect of body coloration and group size on social partner preferences in female fighting fish (*Betta splendens*). *Behavioural processes* **80**: 157-161.
- Bornbusch AH. 1995. Phylogenetic relationships within the Eurasian catfish family Siluridae (Pisces: Siluriformes), with comments on generic validities and biogeography. *Zoological Journal of the Linnean Society* **115**: 1-46.
- Boujard T. 1995. Diel rhythms of feeding activity in the European catfish, *Silurus glanis*. *Physiology & behavior* **58**: 641-645.
- Brännäs E, Lundqvist H, Prentice E, Schmitz M, Brännäs K, Wiklund BS. 1994. Use of the passive integrated transponder (PIT) in a fish identification and monitoring system for fish behavioral studies. *Transactions of the American Fisheries Society* **123**: 395-401.

- Breder CM, Rosen DE. 1966. Modes of reproduction in fishes. Jersey City: TFH.
- Brown C. 2015. Fish intelligence, sentience and ethics. *Animal cognition* **18**: 1-17.
- Brown GE, Smith RJF. 1994. Fathead minnows use chemical cues to discriminate natural shoalmates from unfamiliar conspecifics. *Journal of Chemical Ecology* **20**: 3051-3061.
- Brown GE, Chivers DP, Smith RJF. 1997. Differential learning rates of chemical versus visual cues of a northern pike by fathead minnows in a natural habitat. *Environmental Biology of Fishes* **49**: 89-96.
- Cantalupo C, Bisazza A, Vallortigara G. 1995. Lateralization of predator-evasion response in a teleost fish (*Girardinus falcatus*). *Neuropsychologia* **33**: 1637–1646.
- Carden SM, Boissy RE, Schoettker PJ, Good WV. 1998. Albinism: modern molecular diagnosis. *British Journal of Ophthalmology* **82**:189-95.
- Carol J, Benejam L, Benito J, García-Berthou E. 2009. Growth and diet of European catfish (*Silurus glanis*) in early and late invasion stages. *Fundamental and Applied Limnology/Archiv für Hydrobiologie* **174**: 317-328.
- Copp GH, Robert Britton J, Cucherousset J, García-Berthou E, Kirk R, Peeler E, Stakėnas S. 2009. Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish and Fisheries* **10**: 252-282.
- Cote J, Fogarty S, Weinersmith K, Brodin T, Sih A. 2010. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20092128.
- Cucherousset J, Boulėtreau S, Azėmar F, Compin A, Guillaume M, Santoul F. 2012. “Freshwater Killer Whales”: beaching behavior of an alien fish to hunt land birds. *PLoS one* **7**: e50840

Czarnecki M, Andrzejewski W, Mastyński J. 2003. The feeding selectivity of wels (*Silurus glanis* L.) in Lake Goreckie. *Archiwum Rybactwa Polskiego* **11**: 141-147.

Dadda M, Zandonà E, Bisazza A. 2007. Emotional responsiveness in fish from lines artificially selected for a high or low degree of laterality. *Physiology & behaviour* **92**: 764-772.

Dingerkus G, Seret B, Guilbert E. 1991. The first albino wels, *Silurus glanis* Linnaeus, 1758, from France, with a review of albinism in catfishes (Teleostei: Siluriformes). *Cybiurn* **15**: 185-188.

Dugatkin LA, Wilson DS. 1992. The prerequisites for strategic behaviour in bluegill sunfish, *Lepomis macrochirus*. *Animal Behaviour* **44**:223-30.

Eaton L, Sloman KA. 2011. Subordinate brown trout exaggerate social signalling in turbid conditions. *Animal behaviour* **81**: 603-608.

Elipot Y, Hinaux H, Callebert J, Rétaux S. 2013. Evolutionary shift from fighting to foraging in blind cavefish through changes in the serotonin network. *Current Biology* **23**:1-10.

Elvira B, Almodóvar A. 2001. Freshwater fish introductions in Spain: facts and figures at the beginning of the 21st century. *Journal of fish Biology*, **59**: 323-331.

Engeszer RE, Ryan MJ, Parichy DM. 2004. Learned social preference in zebrafish. *Current Biology* **14**: 881-884.

FAO. 2018. Aquaculture topics and activities. *Fishery Statistical Collections*. In: FAO Fisheries and Aquaculture Department [online]. Rome. Updated 29 December 2015. [Cited 2 March 2018]. <http://www.fao.org/fishery/>

FAWC. 2009. *Farm animal welfare in Great Britain: Past, present and future*. Farm Animal Welfare Council.

Fine ML, Ladich F. 2003. Sound production, spine locking and related adaptations. *Catfishes* **1**: 249-290.

Fine ML, McElroy D, Rafi J, King CB, Loesser KE, Newton S. 1996. Lateralization of pectoral stridulation sound production in the channel catfish. *Physiol. Behav.* **60**: 753-757.

Freyhof J, Kottelat M. 2008. *Silurus glanis*. The IUCN Red List of Threatened Species 2008. Downloaded on 15 November 2017.

Freyhof J, Brooks E. 2011. European red list of freshwater fishes (p. 61). Luxembourg: Publications office of the European Union.

Friard O, Gamba M. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution* **7**: 1325-30.

FSBI. 2002. Fish Welfare. Briefing Paper 2, Fisheries Society of the British Isles, Granta Information Systems, 82A High Street, Sawston, Cambridge.

Gagliardo A, Filannino C, Ioalč P, Pecchia T, Wikelski M, Vallortigara G. 2011. Olfactory lateralization in homing pigeons: a GPS study on birds released with unilateral olfactory inputs. *Journal of Experimental Biology* **214**: 593-598.

Gerlach G, Lysiak N. 2006. Kin recognition and inbreeding avoidance in zebrafish, *Danio rerio*, is based on phenotype matching. *Animal Behaviour* **71**: 1371-1377.

Godin JGJ, Alfieri MS, Hoare DJ, Sadowski JA. 2003. Conspecific familiarity and shoaling preferences in a wild guppy population. *Canadian journal of zoology* **81**:1899-1904.

Griffiths SW, Magurran AE. 1997. Familiarity in schooling fish: how long does it take to acquire?. *Animal Behaviour* **53**: 945-949.

Griffiths SW, Brockmark S, Höjesjö J, Johnsson JI. 2004. Coping with divided attention: the advantage of familiarity. *Proceedings of the Royal Society B: Biological Sciences* **271**: 695.

Haffray P, Vauchez C, Vandeputte M, Linhart O. 1998. Different growth and processing traits in males and females of European catfish, *Silurus glanis*. *Aquatic Living Resources* **11**: 341-345.

Hamilton WD. 1964. The genetical evolution of social behaviour. II. *Journal of theoretical biology*, **7**: 17-52.

Hoare DJ, Krause, J., Peuhkuri, N., & Godin, J. G. (2000). Body size and shoaling in fish. *Journal of Fish Biology* **57**: 1351-1366.

Höglund E, Balm PH, Winberg S. 2000. Skin darkening, a potential social signal in subordinate arctic charr (*Salvelinus alpinus*): the regulatory role of brain monoamines and pro-opiomelanocortin-derived peptides. *Journal of Experimental Biology* **203**: 1711-1721.

Höjesjö J, Johnsson JI, Petersson E, Järvi T. 1998. The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*). *Behavioral Ecology* **9**: 445-51.

HSUS. 2008. An HSUS Report: The Welfare of Animals in the Aquaculture Industry. The Humane Society of the United States Reports: Farm Industry Impacts on Animals.

Huntingford FA, Adams C, Braithwaite VA, Kadri S, Pottinger TG, Sandøe P, Turnbull JF. 2006. Current issues in fish welfare. *Journal of fish biology* **68**: 332-372.

Chivers DP, Brown GE, Smith RJF. 1995. Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour. *Canadian Journal of Zoology* **73**: 955-960.

Jordan LA, Wong MY, Balshine SS. 2010. The effects of familiarity and social hierarchy on group membership decisions in a social fish. *Biology Letters* **6**: 301-303.

Jordão LC, Volpato GL. 2000. Chemical transfer of warning information in non-injured fish. *Behaviour* **137**: 681-690.

- Keller-Costa T, Canário AV, Hubbard PC. 2015. Chemical communication in cichlids: a mini-review. *General and comparative endocrinology*, **221**: 64-74.
- Kohda M, Jordan LA, Hotta T, Kosaka N, Karino K, Tanaka H, Tanyama M, Takeyama T. 2015. Facial recognition in a group-living cichlid fish. *PLoS One* **10**: e0142552.
- Komdeur J, Hatchwell BJ. 1999. Kin recognition: function and mechanism in avian societies. *Trends in Ecology & Evolution* **14**: 237-241.
- Kottelat M, Freyhof J. 2007. Handbook of European freshwater fishes. Publications Kottelat.
- Krause J, Ruxton GD. 2002. Living in groups. Oxford Univ. Press, Oxford
- Lechner W, Ladich F. 2011. How do albino fish hear?. *Journal of Zoology* **283**: 186-192.
- Leliveld LM, Langbein J, Puppe B. 2013. The emergence of emotional lateralization: evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science*, **145**: 1-14.
- Linhart O, Štěch L, Švarc J, Rodina M, Audebert JP, Grecu J, Billard R. 2002. The culture of the European catfish, *Silurus glanis*, in the Czech Republic and in France. *Aquatic Living Resources* **15**: 139-144.
- Loannis L, Lfigenia K, Triantafyllidis A. 2007. Threatened fishes of the world: *Silurus aristotelis* (Agassiz 1856)(Siluridae). *Environmental biology of fishes* **78**: 285-286.
- Magurran AE, Seghers BH, Shaw PW, Carvalho GR. 1994. Schooling preferences for familiar fish in the guppy, *Poecilia reticulata*. *Journal of Fish Biology* **45**:401-406.
- Maiditsch IP, Ladich F. 2014. Effects of temperature on auditory sensitivity in eurythermal fishes: common carp *Cyprinus carpio* (Family Cyprinidae) versus Wels catfish *Silurus glanis* (family Siluridae). *PloS one* **9**: e108583.

Maitland PS, Herdson D. 2009. Key to the marine and freshwater fishes of Britain and Ireland. Environment Agency, Bristol.

Maitland PS, Lyle AA. 1991. Conservation of freshwater fish in the British Isles: the current status and biology of threatened species. *Aquatic Conservation: Marine and Freshwater Ecosystems* **1**: 25-54.

Mateo JM. 2004. Recognition systems and biological organization: the perception component of social recognition. In *Annales Zoologici Fennici* (pp. 729-745). Finnish Zoological and Botanical Publishing Board.

McRobert SP, Bradner J. 1998. The influence of body coloration on shoaling preferences in fish. *Animal Behaviour* **56**: 611-615.

Milinski M, Griffiths S, Wegner KM, Reusch TB, Haas-Assenbaum A, Boehm T. 2005. Mate choice decisions of stickleback females predictably modified by MHC peptide ligands. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 4414-4418.

Miranda A, Almeida OG, Hubbard PC, Barata EN, Canário AV. 2005. Olfactory discrimination of female reproductive status by male tilapia (*Oreochromis mossambicus*). *Journal of Experimental Biology* **208**: 2037-2043.

Mirza RS, Chivers DP. 2001. Chemical alarm signals enhance survival of brook charr (*Salvelinus fontinalis*) during encounters with predatory chain pickerel (*Esox niger*). *Ethology* **107**: 989-1005.

Muleta MG, Schausberger P. 2013. Smells familiar: group-joining decisions of predatory mites are mediated by olfactory cues of social familiarity. *Animal behaviour* **86**: 507-512.

Nadler LE, Killen SS, McClure EC, Munday PL, McCormick MI. 2016. Shoaling reduces metabolic rate in a gregarious coral reef fish species. *Journal of Experimental Biology* **219**: 2802-2805.

Neville AC. 1976. Animal asymmetry. The Institute of Biology's studies on biology. N. 67. London: Edward Arnold

O'Connor KI, Metcalfe NB, Taylor AC. 1999. Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*?. *Animal Behaviour* **58**: 1269-1276.

Paschos I, Nathanailides C, Perdikaris C, Tsoumani M. 2004. Comparison of morphology, growth and survival between *Silurus glanis*, *S. aristotelis* and their hybrid during larval and juvenile stages. *Aquaculture Research* **35**: 97-99.

Pohlmann K, Atema J, Breithaupt T. 2004. The importance of the lateral line in nocturnal predation of piscivorous catfish. *Journal of Experimental Biology* **207**: 2971-2978.

Pohlmann K, Grasso FW, Breithaupt T. 2001. Tracking wakes: the nocturnal predatory strategy of piscivorous catfish. *Proceedings of the National Academy of Sciences* **98**: 7371-7374.

Policansky D. 1982. Flatfishes and the inheritance of asymmetries. *Behav. Brain Sci.* **5**: 262-266.

Proteau JP, Hilge V, Linhart O. 1996. Etat actuel et perspectives de la production aquacole des poissons-chats (Siluroidei) en Europe. *Aquatic Living Resources* **9**: 229-235.

Purdom CE. 1992. *Genetics and fish breeding* (Vol. 8). Springer Science & Business Media.

Randák T, Slavík O, Kubečka J, Adámek Z, Horký P, Turek J, Vostradovský J, Hladík M, Peterka J, Musil J, Prchalová M, Jůza T, Kratochvíl M, Boukal D, Vašek M, Andreji J, Dvořák P. 2013. *Fisheries in open waters*. FROV JU, Vodňany, 434.

Reddon AR, Hurd PL. 2008. Aggression, sex and individual differences in cerebral lateralization in a cichlid fish. *Biology Letters* **4**: 338-340.

- Rodgers GM, Gladman NW, Corless HF, Morrell LJ. 2013. Costs of colour change in fish: food intake and behavioural decisions. *Journal of Experimental Biology* **216**: 2760-2767.
- Rodgers GM, Kelley JL, Morrell LJ. 2010. Colour change and assortment in the western rainbowfish. *Animal Behaviour* **79**: 1025-1030.
- Rogers LJ. 2011. Does brain lateralization have practical implications for improving animal welfare. *Appl. Anim. Behav. Sci.* **127**: 1-11.
- Rogers LJ, Zucca P, Vallortigara G. 2004. Advantages of having a lateralized brain. *Proceedings of the Royal Society of London B: Biological Sciences* **271**: 420-422.
- Rosen DE, Bailey RM. 1963. The Poeciliid fish (Cyprinodontiformes), their structure, zoogeography, and systematics. *Bull. Am. Mus. Nat. Hist.* **126**: 1-176.
- De Santi A, Sovrano VA, Bisazza A, Vallortigara G. 2001. Mosquitofish display differential left-and right-eye use during mirror image scrutiny and predator inspection responses. *Animal Behaviour* **61**: 305-310.
- Scowcroft G, Vigness-Raposa K, Knowlton C, Morin H. 2015. *Discovery of Sound in the Sea*. University of Rhode Island.
- Seppä T, Laurila A, Peuhkuri N, Piironen J, Lower N. 2001. Early familiarity has fitness consequences for Arctic char (*Salvelinus alpinus*) juveniles. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 1380-5.
- Sih A, Cote J, Evans M, Fogarty S, Pruitt J. 2012. Ecological implications of behavioural syndromes. *Ecology letters* **15**: 278-289.
- Siniscalchi M. 2017. Olfactory lateralization. In *Lateralized Brain Functions*. Humana Press, New York, NY. 103-120.
- Slavík O, Horký P. 2012. Diel dualism in the energy consumption of the European catfish *Silurus glanis*. *Journal of fish biology* **81**: 2223-2234.

Slavík O, Horký P, Bartoš L, Kolářová J, Randák T. 2007. Diurnal and seasonal behaviour of adult and juvenile European catfish as determined by radio-telemetry in the River Berounka, Czech Republic. *Journal of Fish Biology* **71**: 101-114.

Slavík O, Horký P, Maciak M. 2015. Ostracism of an albino individual by a group of pigmented catfish. *Plos one* **10**: e0128279.

Slavík O, Horký P, Wackermannová M. 2016. How does agonistic behaviour differ in albino and pigmented fish?. *PeerJ* **4**: e1937.

Slavík O, Pešta M, Horký P. 2011. Effect of grading on energy consumption in European catfish *Silurus glanis*. *Aquaculture* **313**: 73-78.

Sorensen PW, Fine JM, Dvornikovs V, Jeffrey CS, Shao F, Wang J, Vrieze LA, Anderson KR, Hoye TR. 2005. Mixture of new sulfated steroids functions as a migratory pheromone in the sea lamprey. *Nature Chemical Biology* **1**: 324-328.

Sovrano VA. 2004. Visual lateralization in response to familiar and unfamiliar stimuli in fish. *Behavioural Brain Research* **152**: 385-391.

Sovrano VA, Bisazza A, Vallortigara G. 2001. Lateralization of response to social stimuli in fishes: a comparison between different methods and species. *Physiology & behavior* **74**: 237-244.

Sovrano VA, Rainoldi C, Bisazza A, Vallortigara G. 1999. Roots of brain specializations: preferential left-eye use during mirror-image inspection in six species of teleost fish. *Behavioural brain research* **106**: 175-180.

Sugimoto M. 2002. Morphological color changes in fish: regulation of pigment cell density and morphology. *Microscopy research and technique* **58**: 496-503.

Stone R. 2007. The last of the leviathans. *Science* **316**: 1684-1688.

Swaney W, Kendal J, Capon H, Brown C, Laland KN. 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour* **62**: 591-598.

Syväranta J, Cucherousset J, Kopp D, Crivelli A, Céréghino R, Santoul F. 2010. Dietary breadth and trophic position of introduced European catfish *Silurus glanis* in the Tarn River (Garonne River basin), southwest France. *Aquatic biology* **8**: 137-144.

Szabó T, Radics F, Borsos Á, Urbányi B. 2015. Comparison of the Results from Induced Breeding of European Catfish (*Silurus glanis* L.) Broodstock Reared in an Intensive System or in Pond Conditions. *Turkish Journal of Fisheries and Aquatic Sciences* **15**: 379-384.

Takeuchi Y, Hori M, Myint O, Kohda M. 2010. Lateral bias of agonistic responses to mirror images and morphological asymmetry in the Siamese fighting fish (*Betta splendens*). *Behavioural brain research* **208**: 106-111.

Tang-Martinez Z. 2001. The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. *Behavioural Processes* **53**: 21-40.

Thünken T, Waltschyk N, Bakker TC, Kullmann H. 2009. Olfactory self-recognition in a cichlid fish. *Animal cognition* **12**: 717-724.

Ulikowski D, Szczepkowski M, Szczepkowska B. 2003. Preliminary studies of intensive wels catfish (*Silurus glanis* L.) and sturgeon (*Acipenser* sp.) pond cultivation. *Archiwum Rybactwa Polskiego* **11**: 295-300.

Utne-Palm AC, Hart PJ. 2000. The effects of familiarity on competitive interactions between threespined sticklebacks. *Oikos* **91**: 225-232.

van Grouw H. 2006. Not every white bird is an albino: sense and nonsense about colour aberrations in birds. *Dutch Birding* **28**: 79-89.

Vejřík L, Vejříková I, Blabolil P, Eloranta AP, Kočvara L, Peterka J, Sajdllová Z, Chung SH, Šmejkal M, Kiljunen M, Čech M. 2017. European catfish (*Silurus glanis*) as a freshwater apex predator drives ecosystem via its diet adaptability. *Scientific reports* **7**: 15970.

- Velisek J, Wlasow T, Gomulka P, Svobodova Z, Novotny L. 2007. Effects of 2-phenoxyethanol anaesthesia on sheatfish (*Silurus glanis* L.). *Veterinarni Medicina-Praha* **52**: 103.
- Vallortigara G, Andrew RJ. 1994. Olfactory lateralization in the chick. *Neuropsychologia* **32**: 417-423.
- Waas JR, Colgan PW. 1994 Male sticklebacks can distinguish between familiar rivals on the basis of visual cues alone. *Anim. Behav.* **47**: 7–13.
- Ward AJ, Axford S, Krause J. 2003. Cross–species familiarity in shoaling fishes. *Proceedings of the Royal Society of London B: Biological Sciences* **270**: 1157-1161.
- Ward AJ, Hart PJ. 2003. The effects of kin and familiarity on interactions between fish. *Fish and Fisheries* **4**: 348-358.
- Ward AJ, Hart PJ, Krause J. 2004. The effects of habitat- and diet-based cues on association preferences in three-spined sticklebacks. *Behav. Ecol.* **15**: 925–929.
- Ward AJ, Holbrook RI, Krause J, Hart PJ. 2005. Social recognition in sticklebacks: the role of direct experience and habitat cues. *Behav. Ecol. Sociobiol.* **57**: 575–583.
- Ward AJ, Webster MM. 2016. *Sociality: the behaviour of group-living animals*. Springer.
- Ward AJ, Webster MM, Hart PJ. 2007. Social recognition in wild fish populations. *Proceedings of the Royal Society of London B: Biological Sciences* **274**: 1071-1077.
- Westin L. 1998. The spawning migration of European silver eel (*Anguilla anguilla* L.) with particular reference to stocked eel in the Baltic. *Fisheries Research* **38**: 257-270.
- Wisenden BD. 2000. Olfactory assessment of predation risk in the aquatic environment. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **355**: 1205-1208.

Wisenden BD, Smith RJF. 1998. A re-evaluation of the effect of shoalmate familiarity on the proliferation of alarm substance cells in ostariophysan fishes. *Journal of Fish Biology* **53**: 841-846.

Wolcott HL, Ojanuren AF, Barbosa M. 2017. The effect of familiarity on escape responses in the Trinidadian guppy (*Poecilia reticulata*). *PeerJ* **5**: e3899.

Wolter C, Bischoff A. 2001. Seasonal changes of fish diversity in the main channel of the large lowland River Oder. *River Research and Applications* **17**: 595-608.

