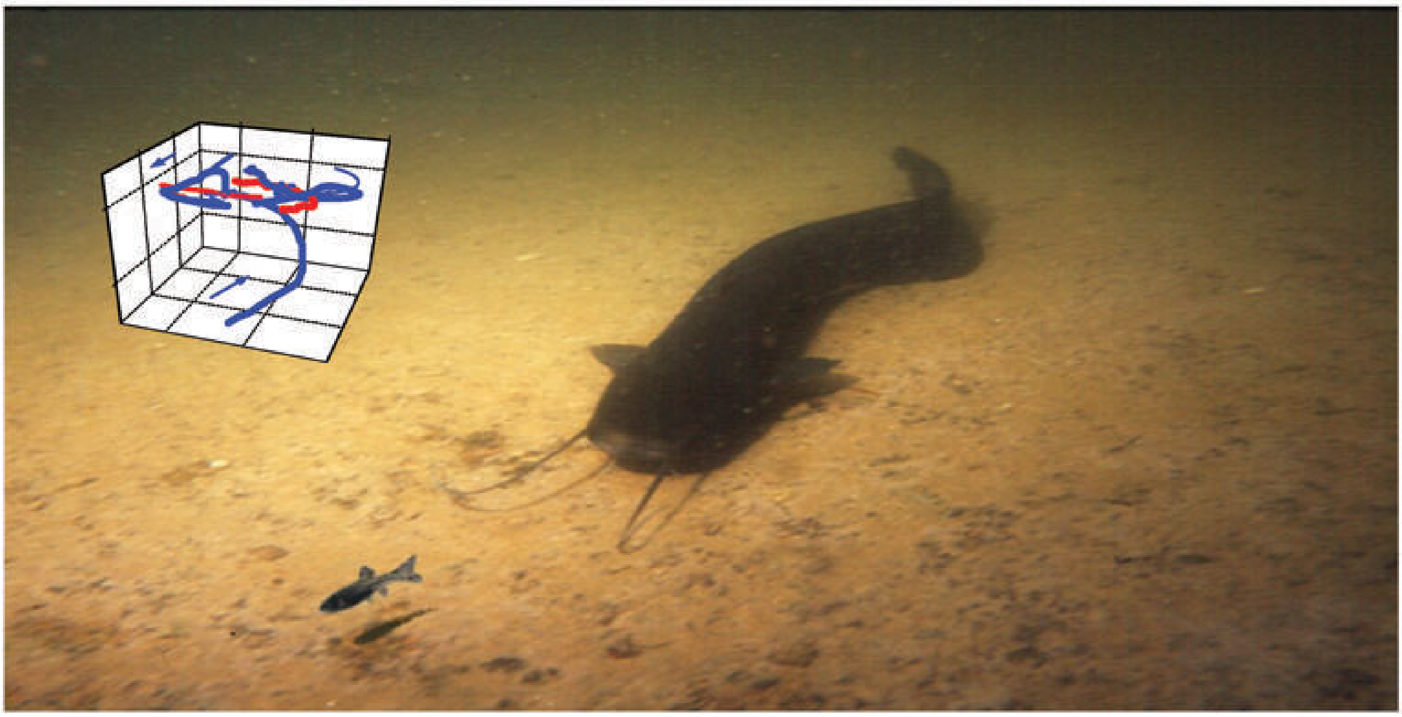
Kirsten Pohlmann

When the night comes:
Non-visual predator-prey interactions in fish



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When the night comes:
Non-visual predator-prey interactions in fish

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1 Introduction

One of the most succinct definitions of ecology was given by Krebs (1972): “Ecology is the scientific study of the interactions that determine the distributions and abundance of organisms“. This includes the level of the individual organism, of populations and communities. The first step in the study of ecology is to make observations and then to seek explain or understand these (Begon et al., 1996). In the mid 1980s freshwater ecologists have started to intensify their interest in trophic interactions and their implications for the structure and dynamics of freshwater communities (Carpenter, 1988; Keerfoot and Sih, 1987). At about the same time a trend to replace phenomenological approaches by more mechanistic ones could be discerned in community ecology in general (Schoener, 1986). Since then many mosaic pieces of information on behaviour and properties of individuals and their implications for populations and communities have been gathered and begin to form a discernible picture on many aspects of aquatic ecology. There are, however, many blank spots in areas of this overall picture, one of which concerns nocturnal interactions of aquatic organisms. This is not surprising since many ecological investigations are spurred by observations. Humans, being terrestrial and primarily visual, have difficulty to observe aquatic phenomena in the dark. To study interactions in the dark we depend on methods to visualise these. This work aims to contribute some important mosaic pieces to fill an aspect of this blank spot, namely interactions between nocturnal piscivorous fish and their prey.

Predator-prey interactions have been shown to have major impacts on different aspects of organisms’ ecology. They influence body morphology and sensory equipment of individuals as well as temporal and spatial aspects of population and community structures (Hart, 1997; Persson et al., 1997). Because evolution ultimately selects for an individual’s fitness, survival (feeding but not being eaten) is essential and under intense selective pressure. In predator-prey interactions the success of the predator means a fatal failure for the prey and the capability of prey to avoid or escape predation can lead to heavy losses for the predator. Thus predator-prey interactions can be expected to be finely tuned in an evolutionary sensory arms race. Both parties are selected to detect their opponent as early and reliably as possible and at the same time to not being detected themselves. In order to understand the impact of predation on population and community structures it is essential to also analyse individual predator-prey interactions. If we do not know predatory strategies we cannot discern antipredator behaviour of potential prey. And if we have no idea about sensory capabilities and behaviour of potential prey fish we cannot understand the adaptive value and evolution of predatory strategies.

1.1 Impacts of predation on spatial and temporal community structures

There is a high abundance of juvenile fish in the littoral of lakes in summer due to the high water temperatures, the availability of refuges and food. Not surprisingly a high abundance of piscivors is also found there. Biotic (e.g. food, macrophytes) and abiotic (e.g. temperature, light) factors are essential players in the trade-off game between safety and growth of organisms under predation pressure. It was repeatedly shown that the presence of predators shifts the habitat utilisation of their potential prey and that this affects multiple trophic levels.

Of the many well studied examples I will just outline two that show spatial and temporal shifts. Diehl and co-workers (all compiled in Diehl, 1994) could show that in the presence of a piscivorous pike juvenile perch increased their use of vegetated habitats where their foraging efficiency and thus their growth was significantly decreased. In turn, macroinvertebrate prey showed higher densities and species richness in vegetated than in not vegetated habitats and were more strongly reduced by perch in macrophyte strands when a pike was present. This shows that the presence of a predator affects several trophic levels and thus has a profound influence on community structures.

The second example is that of zooplankton vertical migration. Chemicals indicating the presence of predators (midges, fish) induce distinct vertical diurnal migrations in daphnids (Kleiven et al., 1996; Ringelberg et al., 1991; von Elert and Pohnert, 2000). In the chemical presence of fish daphnia stays in deeper water layers during day and ascend to the surface when light decreases. Close to the surface they are filter feeding on phytoplankton during night, not needing vision for their own feeding mode but being save from many visually feeding planktivores. The presence of predators reduces the overall phytoplankton consumption of daphnids since in depth where the lack of light prevents fish predation there is also hardly any primary production. The lower temperatures in deeper strata also reduce the growth of daphnia (Loose and

Dawidowicz, 1994). Daphnids thus utilise a spatio-temporal refuge and the presence of fish in the system has an impact on different trophic levels.

Refuges from visual predators (macrophytes, deeper water levels), however, will not necessarily protect from non-visual predators. The trade-offs for potential prey that do not engage in feeding or social interactions during night are certainly different in the dark. Due to their small body size juvenile fish cannot shift to very distant habitats at night and are in fact found near the areas they occupy during day. But since also diurnal prey will have to survive the night we need to gain information on nocturnal predation in order to understand littoral community structures. Many nocturnal piscivors (eel, catfish, burbot) have fairly large body sizes and are thus not too susceptible to predation themselves. Thus for initial steps into this dark unknown realm I restrict my attention to the interaction between juvenile fish and their nocturnal predators, assuming that the distribution of these predators is strongly dependent on the availability of prey.

1.2 Which stimuli can a fish perceive?

In order to address the question which stimuli could be utilised in predator-prey interactions we need to know what properties of its environment an organism can perceive at all. The analysis of sensory organs and systems provides essential information in this respect. Light and spectral sensitivity of a large number of fish have been analysed as well as the development of the visual systems and higher neuronal processing of visual information (Douglas and Djamgoz, 1990). These findings have been compared to natural stimuli and ambient conditions (Gerking, 1994; Lythgoe, 1988). Since this study is concerned with non-visual interactions of fish I will not give any details about vision.

Many fish are equipped with multiple non-visual extraordinarily sensitive senses. There is a large body of literature, therefore in this introduction I will cite summarising book sections and reviews mostly. Original work is cited in all other parts of this thesis.

1.2.1 Mechanoreceptive systems: The inner ear and lateral line of fish

Hearing in the broadest sense is the detection of mechanical energy propagated through the surrounding medium (Coombs and Montgomery, 1999). For a functional consideration this definition should be restricted to exclude substrate vibrations, surface waves, eddies, and turbulence. In the aquatic environment the extended contribution of incompressible flow in the acoustic near field of the source adds additional complexities compared to terrestrial environments (Coombs and Montgomery, 1999). Both incompressible flow (particle motion) and propagated pressure waves are detected by specialised receptor systems.

Acoustic particle motion in fish is detected by one or more otolith organs (saccule, lagena and utricle) found in all fishes (Popper and Fay, 1999). These organs contain a patch of hair cell receptors overlaid by a solid otolith of high density. As sound passes through a fish and brings its tissue into motion, the otoliths are thought to move in a different phase and amplitude due to their greater density and inertia. Thus a relative displacement of the otoliths occurs that is in proportion to acoustic particle motion, having magnitude and direction.

In many fish species, the otolith may also receive a displacement input from the swim bladder or other gas-filled chamber near the ears. Since gas is highly compressible, the swim bladder converts sound pressure into motion that is transferred through tissue to the ear. This input has a magnitude but no direction. The detectable frequencies are in the order of <1-500 Hz by otolith displacement alone and <1-2000 Hz by otolith displacement amplified by gas filled cavities. The maximum sensitivities in most fish lie within the 400 to 1000 Hz range (Ladich, 1999). The better the mechanical coupling between gas bladder and otoliths, the better the hearing. Otophysan fishes have a series of bones, the Weberian ossicles, which acoustically couple the swim bladder to the inner ear, which enhances their sensitivity to high frequencies (up to 5 kHz) and maximum sensitivities in these hearing specialists were found between 400 Hz and 1500 Hz. (Ladich, 1999). The dual sensitivity to pressure and particle movement provides an animal with information about sound source characteristics which may include distance and location (Fay and Megela Simmons, 1999).

Fish posses still another sensory organ, the mechanosensory lateral line, to detect water motions relative to their body, including sound particle movements in the acoustic near field (Coombs et al., 1989). The lateral line organ consists of free neuromasts and canal neuromasts, both containing patches of hair cells sensitive to mechanical deflection. Stimulation of the lateral line can occur when there is a relative movement between the animal and the surrounding water. The free neuromasts react directly to the water motion and due to their asymmetry possess directional sensitivity. The neuromasts embedded in canals respond to motions of the fluid inside the canals that are caused by pressure differences between adjacent pores which connect the inner cavity of the canal with the outer medium. The sensitivity range of the lateral line is different between different fish, both due to neuronal filtering properties and morphological differences as well as physical conditions such as temperature (Coombs and Montgomery, 1992; Coombs and Montgomery, 1999). The frequency range of the lateral line can be as large as <1Hz to 200 Hz with maximum sensitivities below 30 Hz (Coombs and Montgomery, 1999).

Comparing these mechanoreceptive systems there are clear differences: While for the lateral line system the effective stimulus is the differential movement between fish and surrounding water, the otolith responds to whole body acceleration and, mediated through compression of gas filled cavities, to pressure fluctuations. The distance over which a source can be detected is also clearly different: the lateral line system responds to sources in distances of 1-2 body lengths (but see also discussion on wakes below), while the otolith ear alone can detect sources about 10 body lengths away (acoustic near field) and if supplemented by air filled cavities, even 100 body lengths (acoustic far field) (Coombs and Montgomery, 1999).

1.2.2 Chemoreceptive systems: olfaction, gustation, and solitary chemosensory cells

The peripheral olfactory (smell) organ of fish is located in the nasal sac and is highly variable in morphology. Teleost fish have paired olfactory sacs with one or two nares (external openings) each. The olfactory epithelium inside the olfactory sac is arranged in a rosette, which has a variably folded surface, increasing surface area. This olfactory epithelium has an extremely high density of receptor cells (as many as 5×10^5 mm^{-2} receptors) that bind to chemicals and transfer external information directly to the brain (Zeiske et al., 1976). There are two morphologically distinct olfactory receptor cell types in teleosts: ciliated and microvillar (Satou, 1992).

In the gustatory (taste) system sensory cells (SSCs) are organised in taste buds. They are located in the mouth cavity and pharynx, on the gills, barbels, fins, and, in some species, on the entire body surface. At least three distinct cell types have been identified: light and dark microvillar cells and basal cells. The latter are thought to be interneurones and may have a mechanosensory function, the light cells are gustatory and the dark calls may have supporting function (Reutter, 1992). The taste system is devised into two subsystems (facial and vagal) by different enervation, each serving different phases of the feeding behaviour (for more details see chapter 3).

The third and least well understood chemosensory system of fish is that of solitary chemosensory cells (SCC). It consists of differentiated epidermal cells, which closely resemble gustatory receptor cells, were shown to be chemosensory, and are not organised in discrete end organs (Whitear, 1999). They are found in the external skin, gills, in the mouth, and pharynx in many teleosts. Some cells of the same structure that belong to this third system are also found within taste buds.

Studies on sensitivity and specificity of these chemosensory systems are conducted with a limited number of stimulants (reviewed by Hara, 1992; Marui and Caprio, 1992). Physiological studies of chemical stimulants have centred on amino acids and, more recently, steroids, prostaglandins, and bile salts. For the best studies amino acids olfactory threshold sensitivities of 10^{-7} and 10^{-9} M and concentration-response relationships covering 6 to7 log unit have been documented (Hara, 1992). Relatively few fish species have been studied with respect to gustation. Amino acids and nucleotides are particularly stimulating to gustation. Responses vary greatly among species, both in terms of sensitivity and specificity. Gustatory threshold concentrations for the facial system were found in the µM to nM range (Marui and Caprio, 1992). SSCs were reported to be narrowly tuned to dilutions of fish mucus and bile (Kotrschal, 1996).

1.2.3 Electroreception

Some fish can also detect electrical signals in the water. Catfish belong to the few bony fish that possess passive electroreception and I will limit my description to this. For reviews see Finger (1986)and Kalmijn (1988). Passive electroreception means that detected fields are of extraneous origin. Electroreceptive organs are part of the lateral line organ (Bullock, 1974; Kramer, 1996; Szabo and Yvette, 1974) and organised in small pit organs (Dijkgraaf, 1968). The receptors are distributed across the entire surface of catfish with the exception of the barbels (Peters et al., 1974). Ampullary electroreceptor cells and their supporting cells form the sensory epithelium lining an ampulla found at the end of a transepidermal canal that opens to the outside. This canal is filled with a jelly of low resistivity and is short in freshwater fish.

Ampullary organs are voltmeters that are sensitive to both, DC and low frequency AC fields. Catfish could be trained to detect voltage gradients down to $1\mu V\ cm^{-1}$ (at 0.5 nA cm^{-2}) in uniform DC fields (Kalmijn 1974) and catfish can sense the polarity of such fields (Roth, 1972).

1.3 Which cue may give away a predator or prey?

The next step in our consideration of non-visual predator-prey interactions in fish is the question which cues of a potential predator or prey fish the respective opponent could detect with its above described sensory systems. Most physiological studies have been conducted with simple and artificial stimuli, so one has to compare the obtained sensitivities to the quality and magnitude of natural stimuli emanating from fish to deduce potential detection mechanisms. Due to the often complex nature of natural stimuli this is possible only to a limited extend. Future physiological studies should therefore aim to test responses to stimuli occurring in the natural environment of the respective fish.

1.3.1 Acoustic and hydrodynamic stimuli

Apart from studies of vocalisation in fish there are hardly any studies on “unintentional sounds” produced by fish that might elicit responses of the otolith organ (Zelick et al., 1999). A slow swimming fish cannot be detected by another’s otolith organ but sounds that are created by rapid movements fall within its sensitivity (Breithaupt, unpublished data). Such rapid movements include fast starting motions by fish or the snapping by predators (Bublitz, 2000; Breithaupt, unpublished data). Startle responses can have frequency components of up to at least 100 Hz (Bleckmann et al., 1991). There are some speculations that the evolution of the Weberian apparatus was driven by predation pressure (Ladich, 1999; Travolga, 1981). Rogers hypothesised that fish might screen for objects through gaps in ambient noise, since any sound-scattering object could be detected against the ambient acoustic background (Rogers, 1986). Thus also soundlessly approaching predators or prey could be detected and possibly information on their size and location could be obtained. This possibility has yet to be investigated.

The hydrodynamic stimuli caused by fish swimming in different modes have been studied in detail (Bleckmann et al., 1991; Hanke et al., 2000; McCutchen, 1977; Müller et al., 2000; Wardle and Videler, 1980) and the resulting vortices were found to be well within the range of fish lateral line perception (Bleckmann et al., 1991). The wake of a fish holds information on speed, direction, swimming mode, and size of the fish in its hydrodynamic structure (Bleckmann et al., 1991). Particle image velocimetry revealed that in still water a wake persists over a 3 minute period (Hanke et al., 2000).

Large swimming fish such as predators build up a bow wave in front of them which could be utilised by prey fish to escape before an attack is initiated. The dimension of such a bow wave is dependent on the swimming speed and the shape and size of the fish.

A different type of wake that can elicit lateral line responses is caused by a stationary object in flowing water. Fish resting on the ground in ambient flow could thus also be detected hydrodynamicly.

1.3.2 Chemical cues

Since the natural environment is full of obstacles the world of fish is full of wakes created by all sorts of inanimate and animate sources chemical information may be useful to distinguish wake sources of interest (e.g. potential predators or prey). Since physiological studies with natural chemical stimulus mixtures are few we will turn to behavioural studies of chemosensory capabilities of fish. These have shown that fish can chemically make very fine distinctions between other fish, e.g. distinguish other species, recognise kin and familiar fish. A fish can chemically recognise a predator by prior learning or in association with alarm substance exudates from its diet (Mathis and Smith, 1993). If diet can be recognised also predators could determine that a detected fish is planktivorous and thus a potential prey and at least no danger. The intensity of odour might be an indication of the size of the source fish because the amount of released chemicals is depending on the surface area. Alarm substance is discussed in more detail below.

1.3.3 Electric cues

Many freshwater animals produce low frequency AC currents or modulated DC fields that are well within the range detectable by ictalurid catfish (Finger, 1986; Peters and Bretschneider, 1972; Roth, 1972).

1.4 Known stimuli in nocturnal piscine predator-prey interactions

The knowledge of predator-prey interactions in fish reflects our biased interest for visual interactions, although in aquatic habitats vision is often limited. There are, however, some findings on non-visual interaction which indicate the importance of the above discussed cues. One has to keep in mind that in different phases of a predator-prey interaction different stimuli and strategies may be employed. A potential prey organism could minimise the encounter probability with a predator by area avoidance, by reduced locomotion or by reduced emission of stimuli that may be detected over some distance. Once the prey has been detected, it could deter the predator or escape, if it perceives the danger. A predator has to counter these strategies once it has been discovered, thus it should aim to avoid disclosure. Cues that are emanating from the capture process itself may serve to inform other potential predators or prey of a nearby predation. They are part of the original predator-prey interaction only if it has any effect on this.

1.4.1 Acoustic and hydrodynamic stimuli

The least of all behavioural evidence of all above mentioned potential cues in predator-prey interactions is in the field of stimuli exciting the otolith organ of non-vocalising fish. As Myrberg points out it is theoretically possible that acoustic interactions play a role in the attraction of prey or the deterrence of predators but there is no behavioural evidence (Myrberg, 1981). In playback experiments juvenile cyprinids showed a reaction that resembles the fright reaction elicited by alarm substance when being exposed to a sound recorded from a pikeperch capturing small prey fish (Bublitz, 2000). This could inform other nearby fish that there is an active predator in the area and, since juvenile fish mostly form loose aggregations in the dark, could hint to secondary predators that there may be more prey in the area.

Compared to the immense body of physiological studies on the mechanosensitive lateral line of fish there is an amazing lack of behavioural studies showing the significance of hydrodynamic stimuli in the detection of moving prey (Enger et al., 1989; Montgomery and Hamilton, 1997). Wunder reports that nocturnal predators, eel and burbot, with ablated eyes followed the wake created by moving a wooden stick through the water (Wunder, 1927). The lateral line was further shown to be involved in feeding of fish on zooplankton (Hoekstra and Janssen, 1985; Montgomery, 1989) or benthic invertebrates

(Montgomery and Hamilton, 1997; Montgomery and Milton, 1993) and of surface feeding fish (Bleckmann, 1985; Bleckmann, 1988). There are only two studies in which the involvement of the lateral line was tested in piscivores, both using diurnal visual predators. Blinded pike, *Esox lucius*, which are visual ambush predators, attack live fish from distances of up to 10 cm only if their lateral line is intact (Wunder, 1927). Intact bluegills, *Lepomis macrochirus*, attack live fish in the absence of visible light only when it is moving or after touch (Enger et al., 1989). There is no published behavioural evidence on the role of lateral lines in initiating escape movements of prey.

1.4.2 Chemical interactions

In recent years evidence accumulated that chemical stimuli play a major role in aquatic predator-prey interactions (for reviews see Chivers and Smith, 1998; Kats and Dill, 1998). The best studied non-visual interaction is the alarm substance system. Not only does alarm substance label predators and warn nearby conspecifics, it also attracts secondary predators and thus increases the escape probability of the captured prey (Chivers and Smith, 1998; Mathis et al., 1995; Smith and Lemly, 1986). There are very few studies of fright behaviour of potential prey fish elicited by alarm substance in the dark and alarm reactions were reported to be absent (Jachner, 1995).

Most of the studies in predatory fish-fish interactions deal with the prey’s perspective and all of the predators investigated were predominantly visual (pike, perch). The importance of olfaction over vision in nocturnal predators is indicated in the large surface area of the olfactory epithelium relative to the area of visual cortex (Teichmann, 1954) and in the dense coverage of large parts of the body with taste buds. In catfish, used as predators in the present study, chemical receptors are present in high densities on the whole body surface (Atema, 1971).

1.4.3 Electric fields

It was demonstrated that catfish can use electroreception alone to locate live prey fish (Kalmijn, 1974) and that its ampullary electroreceptors respond to the potentials generated by small live fish at a distance of 5-10 cm (Roth, 1972).

1.5 Aims of this study

On the basis of physiological measurements on the properties of sensory organs and measurements of natural stimuli one can try to deduce a picture of the animal's world and interpret its behaviour. By skilfully designing experiments one can find out that animals are able to perform certain tasks. The experiments have to be designed in a way that the interpretation of the results is unambiguous. But only in a behavioural context we can start to understand the development of sensory systems and the evolution of sensory capabilities.

In this study I examine interactions of nocturnal predators and their prey in the dark. The first chapter deals with the hypothesis that catfish (*Silurus glanis*), a nocturnal predator, may utilise chemical and hydrodynamic information in the wake of a swimming fish to localise its prey. To test this hypothesis I developed a mathematical algorithm to analyse path similarities on a quantitative basis. I was using a non-sympatric prey (guppy, *Poecilia reticulata*) here. The second chapter discerns the relevant stimulus for tracking a prey's wake. The third chapter addresses the question whether wake tracking is also employed when capturing sympatric, swifter prey. This third chapter further compares the predatory strategy of catfish to that of another prevalently nocturnal predator, the burbot (*Lota lota*). I offered burbot a variety of sympatric prey species to discern potential reasons for preferences found in the field.

Since a predator-prey relationship is a dynamic interaction co-evolving under strong selective pressure, I also looked at the prey's side. In chapter 4 the other side of the interaction, the prey, is considered. Simulating a risk of predation by adding alarm substance I determined behavioural changes and, from the knowledge of predatory sensory systems and one nocturnal predation strategy, discuss the observed reaction in respect of its antipredator function.

Having considered both sides of a nocturnal predator-prey interaction under lab conditions the next question is how important the observed strategies are under natural conditions. Unfortunately, infrared illumination used in my laboratory studies is not applicable in larger dimensions and with structures obliterating vision. Thus I developed a method to automatically track up to 10 fishes three-dimensionally in a larger set up. This technique will enable future studies of predator-prey interactions in the absence of light under more natural conditions.

Each section of this thesis has been compiled as an independent publication. Therefore, some parts may be redundant. The following publications have been published slightly altered or submitted for publication:

Pohlmann, K., Grasso, F. W. and Breithaupt, T. (2001b). Tracking wakes: The nocturnal predatory strategy of piscivorous catfish. *PNAS* 98, 7371-7374.

Pohlmann, K., Atema, J. and Breithaupt, T. The importance of the lateral line in nocturnal predation of piscivorous catfish. ***in review***.

Pohlmann, K. and Breithaupt, T. Creepy nights: alarm substance elicits anti-predator reaction in juvenile dace in darkness. ***submitted***

Pohlmann, K. and Breithaupt, T. To see or not to see - predatory strategies of two nocturnal piscivors. ***submitted***.

My co-authors in these publications contributed, besides helpful discussions, the following to this thesis:

Frank W. Grasso performed part of the behavioural trials of chapter 2 after I had developed the set up and designed the protocol. Jelle Atema performed the brain lesions of the catfish utilised in chapter 3.

Harald Richter developed the hardware of the telemetry system described in chapter 6 and Willi Nagl helped with data analysis and with the algorithm development for the telemetry system.

2. Tracking wakes: the nocturnal predatory strategy of piscivorous catfish

Swimming fish leave wakes containing hydrodynamic and chemical traces. These traces mark their swim path and could guide predators. We now show for the first time that nocturnal European catfish (*Silurus glanis*) locate a piscine prey (guppy; *Poecilia reticulata*) by accurately tracking its three-dimensional swim path prior to an attack in the absence of visible light. Wakes that were up to 10 s old were followed over distances up to 55 prey body lengths in our set-up. These results demonstrate that prey wakes remain identifiable sufficiently long to guide predators and to considerably extend the area in which prey is detectable. Moreover, wakes elicit rear attacks, which may be more difficult to detect by prey. Wake tracking may be a common strategy among aquatic predators.

2.1 Introduction

When an animal swims, chemical and hydrodynamic stimuli persist in its wake for some time after it has left the vicinity (Dusenbery, 1992; Hanke et al., 2000). Previous studies on predatory fish using olfactory or mechanosensory cues to localise moving prey are few in number and indirect (Enger et al., 1989; Montgomery and Hamilton, 1997). Most studies on predator-prey interactions in fish have used predominantly visual predators under well-lit conditions (Gerking, 1994). The niches of many piscivorous fish, however, require them to hunt at night or at depths where the limited penetration of solar, sidereal, or lunar illumination limits the utility of visual senses (Helfman, 1993). We hypothesised that in these circumstances wakes left by prey fish are used by predatory fish to detect and track their prey in three dimensions (3D), analogous to the way in which dogs or snakes follow the two-dimensional tracks left by their terrestrial prey (Thesen et al., 1993; Webb and Shine, 1992). In order to test this hypothesis we analysed the predatory strategy of a nocturnal catfish (*Silurus glanis*) as it found and attacked swimming prey fish (guppies, *Poecilia reticulata*). The use of a prey's wake can be distinguished from visual, acoustical, and electrical tracking of prey by path analysis. In all but wake tracking the predator perceives the instantaneous location of its prey and will approach it directly or in an arc, intercepting the prey's path (Kalmijn, 1988; Ohlberg et al., 2000). An indication, therefore, of wake tracking is the similarity of the paths of prey and predator through space with a significant time lag.

2.2 Materials and Methods

We used a video-based infrared illuminated system maintaining both prey and predator in visual blackout conditions and allowing us to make 3D evaluations of their swim paths. This consisted of a glass test aquarium (120 cm l x 60 cm w, filled to a height of 40 cm) illuminated by infrared back lighting. The infrared used was in the range 810-950 nm (maximum at 870 nm) which is outside the range of absorption of the visual pigments of fish (Dartnall, 1975). Catfish conditioned to react to visual stimuli do not react under infrared illumination, confirming that they cannot see in infrared (pers. observation). Fish behaviour was recorded on digital video using two IR-sensitive cameras from different directions. The two recordings were synchronised accurate to the frame. Guppies (total lengths 2.0 to 5.1 cm) were chosen as prey for their slow and clumsy swimming behaviour and for their low tendency to swim or rest close to walls. Guppies use undulatory and push and coast swimming. The wakes caused by both of these swimming modes are well described (Hanke et al., 2000; McCutchen, 1977; Müller et al., 2000). Four different catfish were used as predators, total lengths 20-25 cm. They were accustomed to feeding on live piscine prey.

Each trial started after the catfish had been acclimated in the experimental tank for at least one hour in darkness. The experimental room was entered through a double curtain to ensure total darkness and one individual guppy was added with a small amount of water (< 50 ml) into the middle of the experimental tank. Five minutes after the prey had been consumed (viewed on monitors next door) the next prey was added. A trial ended when 10 prey fish had been consumed or was aborted when the added prey fish was not consumed within 20 minutes.

2.2.1 Attack characterisation

All sequences leading to attacks of the predator on a prey were carefully analysed from the two video recordings. All captures and snapping movements of a catfish directed at a guppy less than 1.5 cm away were considered attacks. The direction from which the guppy was attacked (top, below, sides, front, behind) was determined for each sequence. The direction of attacks did not change with the number of prior attacks (nominal logistic regression, p = 0.45). Nominal logistic regression is used to determine the effect of one or more predictors on a nominal (i.e. not quantitative) dependent variable. There were no significant effects of guppy gender or its total length or of catfish ID on the direction of attacks (tested simultaneously by nominal logistic regression, $p \geq 0.38$). Therefore all data were pooled for subsequent analyses.

We classified all attacks into three categories: 1) *path following*: the predator swam along the same path as the prey, eventually attacking it; 2) *head-on encounters*: the predator encountered the moving prey without prior path overlaps; 3) *attacks on stationary guppies*.

2.2.2 Quantitative path analyses

In order to determine whether catfish were actually following the wakes of their prey we digitised (at 25 Hz; Adobe Premiere 5.1) sequences with attacks occurring away from the walls to avoid path convergence resulting from both fish swimming along the wall. We chose 22 attacks classified as path following; for both other types all attacks away from the walls were digitised. The digitised sequences ended with the attack or capture and started two seconds before the predator seemed to respond to the presence of the prey. To digitise swimming paths we tracked the position of the tip of the heads of both predator and prey using motion analysis software (WINanalyze 1.1, Weinberger, Karlsruhe).

The resulting 3D swim paths of predator and prey were smoothed by a running average over 10 points to eliminate predator head movement and tracking inaccuracies. These digitised swim paths were then plotted (examples see Figure 2.1 and 2.2). To establish a quantitative comparison of swim paths independent of the swimming velocities of predator or prey new points were set at regular intervals of 2 mm on each path. In order to determine if the predator had been swimming along the path of the prey the swimming direction in each point of the predator's path was subtracted from the direction of the closest point of the prey's path that occurred simultaneously or prior.

Indices of path similarity were computed from the distribution of these differences in swimming direction for each pair of swim paths. As indices we used the medians of the distributions to express central tendency and quartile differences (75%-25% quartile) to express the spread of the distributions. Separate indices were computed for the medians and quartile differences in the orthogonal xy-and xz-planes for each pair of swim paths. Fish swimming along the same path, regardless of how complex or convoluted, should have small differences (medians around zero and small quartile differences) in swimming directions, while for fish swimming on independent paths absolute values of these parameters should be considerably larger.

Nearest neighbourhood discriminant analysis (k=3) was used to determine the reliability of our three predetermined attack categories. This analysis was calculated on the basis of medians and quartile differences of distances between nearest points and difference in swimming direction. The proportion of mis-classification was estimated using the cross-validation approach, which is suitable for low and unequal sample sizes (Lachenbruch and Mickey, 1968; SAS, 1993).

All calculations, and the discriminant and cross-validation analyses (PROC DISCRIM, METHOD=NPAR) were done using SAS 8; nominal logistic regressions and Chi^2 tests for the goodness of fit were performed in JMP 3.15.

2.3 Results

Of the 94 observed attacks 59 resulted in successful captures of guppies. 75 (80%) of all attacks occurred on moving prey, which is significantly higher than expected from the proportion of time guppies spent swimming (43% of total time, averaged from 8 arbitrarily chosen sequences of 31 min total duration; Chi^2 test for goodness of fit; $p<0.0001$).

Most attacks were initiated from behind the prey fish (46% compared to 21% from the front, 9% from the two sides, 6% from above, and 18% from below). This proportion is significantly higher than expected if predators had no preferred attack direction (16.7 %, Chi^2 test for goodness of fit; $p<0.0001$). 95% of all rear attacks were directed toward moving prey.

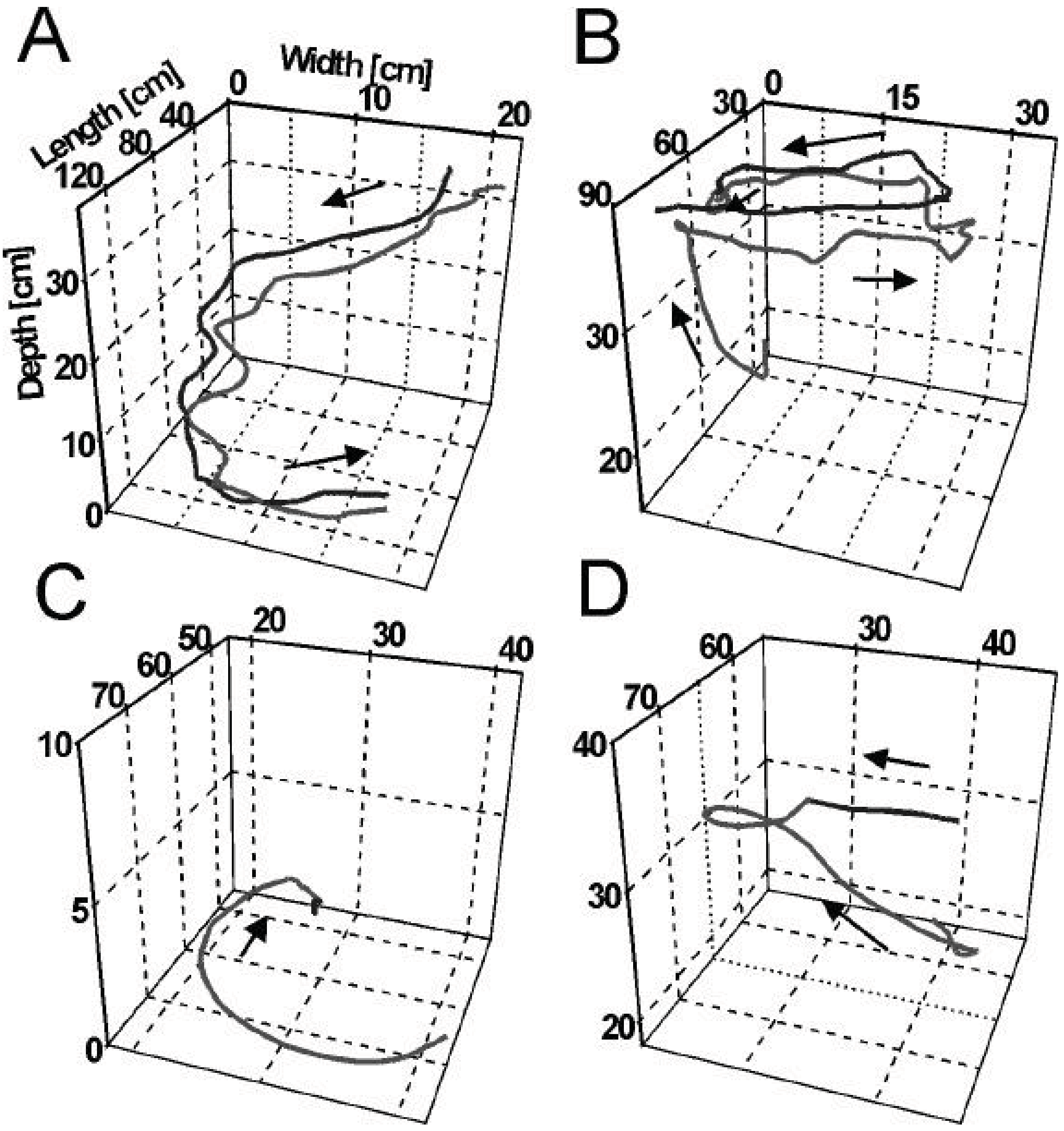

Figure 2.1: Examples of smoothed three dimensional swim paths of predator and prey prior to attacks classified as: **A+B** wake following, **C** attack on stationary guppy, **D** head-on encounter. Grey: predator, black: prey. The numbers depict cm and correspond to calibrated positions in the test tank. Arrows indicate the swimming direction. In A the prey was captured. The three planes drawn do not depict the walls of the tank: the bottom was at depth= 0 cm, the surface at depth= 40 cm, the walls at length= 0 and 120 and at width= -5 and 55 cm. Note different x, y, and z scales.

Of the observed 94 attacks 57 were categorised as path following, 23 as head-on encounters and 14 as attacks on stationary guppies. The categorisation was confirmed graphically by plotting all digitised swim paths in 3D. Figure 2.1 shows examples of smoothed swim paths of predator and prey prior to attacks of all three categorisations. Figure 2.2 depicts the spatio-temporal relations between predator and prey in another example categorised as path following. The positions are indicated at 5 points in time: start and end and 1-3, for catfish (“c”) and guppy (“g”).

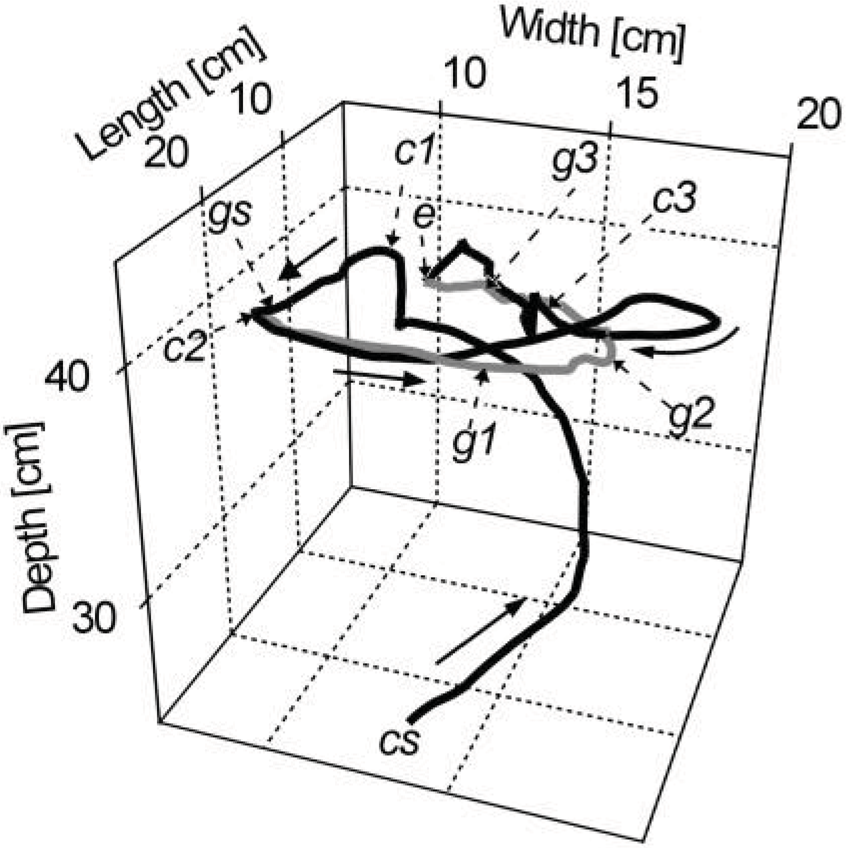

Figure 2.2: 3D plot with temporal information of an attack categorised as wake following. Black: predator, grey: prey. The numbers depict cm and correspond to calibrated positions in the test tank. Coloured arrows indicate the swimming direction. Three points in time (1= 11.3 s, 2= 8.6 s, and 3= 3.4 s prior to the attack) were chosen to indicate the locations of both fish: c1-c3 correspond to positions of the catfish, g1-g3 to those of the guppy. E.g. c2 and g2 are synchronous positions. Also, the first (cs and gs) and last (e) points of both paths are at the same time. The track following appears to begin when the prey is at g2 and the predator at c2. Note different x, y, and z scales.

Indices of path similarity computed from the distribution of the differences in swimming direction supported our classification: The medians and spread of the differences in swimming direction of attacks classified as path following were small and much lower than those of the head-on encounters and attacks on stationary guppies (Figure 2.3). Thus, in sequences categorised as wake following predator and prey were predominantly swimming in the same direction when, with a delay, they occupied the same location.

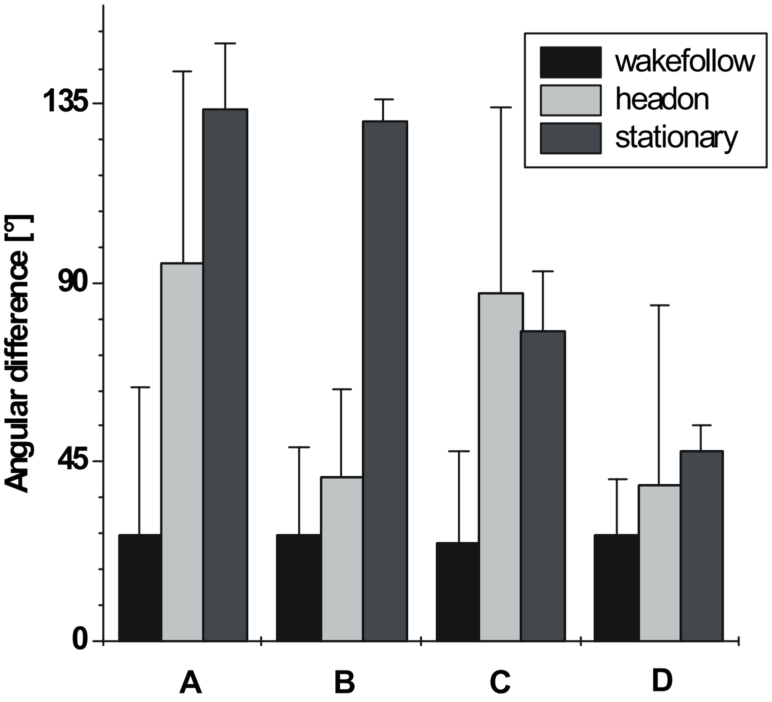

Figure 2.3:Means and standard deviations of differences in swimming direction of predator and prey prior to attacks comparing three attack categories: path following, head-on encounters and attacks on stationary guppies.
A: Medians in xy-plane, B: Quartile differences in xy-plane, C: Medians in xz-plane, D: Quartile differences in xz-plane.

Nearest neighbourhood discriminant analysis and cross-validation further confirmed our categorisation on the basis of quantitative criteria. Of the 34 digitised swim paths (22 path following, 7 head-on encounters, 5 attacks on stationary guppies) only the two shortest were mis-classified: one path following was classified as a head-on encounter, one head-on encounter as an attack on a stationary guppy.

These results confirm that in the majority of all attacks catfish were swimming along the same path as their prey prior to the attack.

The digitised sequences showed that catfish followed the wake of their prey for up to 121 cm (~55 prey body-lengths) and for as long as 33 s with maximal distances of 40 cm between animals in spite of the confined space of our aquarium. The median length of tracked guppy paths was 47 cm. The path of the prey was up to 10.3 s old when encountered and subsequently followed by the predator. Distances between the prey and predator ranged from 40 to 6 cm (median 12 cm) at the onset of tracking. The median distance during all digitised tracking sequences was 7.6 cm with distances gradually decreasing as the predator approached the prey (see Figure 2.2).

2.4 Discussion

The fact that the proportion of fish being attacked when moving is significantly larger than the proportion of time guppies spend moving indicates that catfish find moving guppies easier to detect and localise. This could imply wake detection but also the use of vision, hearing, and other senses that detect the instantaneous position of moving prey. However, we discovered here that moving fish were predominantly attacked from behind, that distances between fish at the onset and during path following were several prey lengths, and that the majority of attacks occurred after path following. This makes it most likely that the predator followed chemical/hydrodynamic cues in the wake of the prey. Chemical cues in the wake could be detected by olfaction or the extensive sense of taste; the latter is used by similar catfish in localising non-moving food (Atema, 1971a). Hydrodynamic cues could be detected by the lateral line.

As alternatives to using hydrodynamic and/or chemical cues marking *past* prey positions in the wake the predator could have used visual, acoustic, or electric cues radiating directly from the swimming prey, revealing its *instantaneous* position. Predators perceiving the instantaneous position of a prey would not follow more or less convoluted trails, i.e. past positions, over several prey body lengths if they knew the actual prey location and could make a direct attack. Predatory strategies other than wake tracking would thus result in different swim paths or different spatio-temporal relations between predator and prey as further explained below. Catfish are known to have a keen sense of hearing (Fay, 1988) and passive electroreception (Finger, 1986; Peters and

Wijland, 1974). These as well as vision could be used to determine the instantaneous prey position.

Catfish do not appear to use their eyes for food detection (pers. obs. and Atema, pers. com.) and, in addition, we did our experiments under infrared illumination eliminating visual cues in the spectrum generally perceivable by fish. Observations made when maintaining catfish in the lab indicate that catfish in general do not orient toward the visual image of food even in visible light. Acoustically guided attacks toward a target that is emitting sound continuously or in pulses (i.e. with every tail beat) are expected to come from any side but not preferably from behind the prey. Acoustic stimuli have been presumed to occur during swimming (Hawkins and Myrberg, 1983). In other experiments we introduced a highly sensitive hydrophone (Brüel & Kjaer, Type 8101) into the tank. However, we never succeeded in recording any sounds from small fish as used in the present experiment. In addition, in our experimental aquarium the background noise originating from pumps and cooling systems were so high (90 dB re 1 µPa, 0-200 Hz) that they would have masked subtle acoustic stimuli. Therefore, we conclude that neither visual nor acoustic stimuli were used to guide the wake following of the catfish.

Fish are surrounded by a dipole-like electric field detectable by catfish at about one prey body length (Kalmijn, 1988). When swimming, they also generate local hydrodynamic cues distinct from the wake (i.e. dipole-like flow fields (Kalmijn, 1988)). Neither of these fields is strongest behind the prey.

Swim paths of prey and predator would also be similar, at least over short distances, if the predator continuously sensed the instantaneous location of the moving prey and followed behind cautiously and closely or if the prey sensed the nearby predator and swam away with the predator again following immediately. The prey upon sensing the predator would be expected to react with escape movements. Rapid escape movements of the prey prior to an actual attack never occurred.

At greater distances (i.e. a few prey lengths) between predator and prey the predator should cut corners, resulting in more rapid turns: Instead we observed gradual curves along the trail of the prey.

Finally, the distance between predator and prey along their paths gives important clues to the sensory information most likely used by the predator. As depicted in Figure 2.2 at time 1 (c1, g1) the distance between predator (c1) and prey (g1) is smaller (distance = 6 cm) than at time 2 (c2, g2, distance = 10 cm). If the catfish used any form of instantaneous position detection (vision, audition, or the local electric or hydrodynamic stimulus fields) and not the wake, the predator should turn towards the prey at time 1 and not continue straight until hitting the previous path of the prey.

Therefore, the high proportion of observed rear attacks and the similarities in swim paths when fish were still several prey lengths apart can neither be explained by random encounters, nor by visual, electrosensory, or acoustic orientation. Wake tracking is the most parsimonious explanation for the observed predatory behaviour.

Tank constraints may have limited wake detection. Flow visualisation using small particles revealed that the disturbances created by the swimming catfish overpowered the smaller wakes of the prey, thereby limiting the possible tracking distance. The small test aquarium increased the probability of random encounters and caused wake reflections off the walls. Despite these constraints wake following was the most frequent occurrence preceding an attack.

Hanke *et al.* showed that in still water a wake can be measured by particle image velocimetry over a 3 minute period and conclude that fish should be able to derive directional information from a 60 s old wake (Hanke et al., 2000). We expect that the distance and duration over which a wake can be detected under quiet natural conditions with modest background flow are higher than the 10 s found in our experiment with fewer reflections and predator-caused perturbations than in our tank.

In the wake of a swimming fish, there is hydrodynamic and chemical information (Atema, 1996). The hydrodynamic stimuli caused by fish swimming in different modes have been studied in detail (Bleckmann et al., 1991; Blickhan et al., 1992; McCutchen, 1977; Müller et al., 2000). The hydrodynamic structure of a wake may hold information on direction, swimming mode, and size of the fish (Bleckmann et al., 1991; Hanke et al., 2000). Because there are characteristic changes during the ageing of hydrodynamic structures (Hanke et al., 2000), it should be possible for a fish to estimate how long ago another fish had been there. The lateral line is sensitive enough to detect these stimuli and filters the relevant details (Bleckmann, 1994; Engelmann et al., 2000).

Chemical signals contained in the wake provide information about identity, and possibly distance and direction of the prey. Size can be assessed from the expansion. Distance and direction are coded in steepness of the chemical gradients in dispersing odour patches (Atema, 1996). In catfish, chemical (taste) receptors are present in high densities on the whole body surface (Atema, 1971b). Gustation is their major sense involved in locating and ingesting non-moving food (Atema, 1971b) and they exhibit true gradient search to locate non-moving food items in stagnant water (Bardach et al., 1967). Direction and age of the odour trail can be assessed by instantaneous chemical comparison using bilateral receptors (e.g. on the barbels) or temporal (sequential) comparison with only one sensory organ (Atema, 1996). Our catfish showed an enhanced interest in places where the prey had spent extended time intervals before. It is possible that in these regions chemical stimuli had accumulated. It is not known if catfish use olfaction or taste for wake tracking. Future ablation experiments will reveal whether smell, taste and/or hydrodynamic stimuli provide the sensory cues utilised during wake tracking.

Wakes are a ubiquitous consequence of physical objects moving through a fluid. Doall *et al* showed that copepods follow their mating partners using chemical cues in the wakes (Doall et al., 1998). Our study shows that at least one species of teleost can make use of the hydrodynamic/chemical cues in the wake to track its prey. We suspect that exploitation of these cues is common among large animals that track moving prey through water.

Denhardt *et al.* showed that harbour seals can be trained to follow the hydrodynamic trail produced by a propeller driven mini-submarine using their whiskers for sensing the water movements (Dehnhardt et al., 2001). The wakes of fish schools condition a much larger area than that of individual fish and provide even more conspicuous tracks to be used by predators (Pitcher and Parrish, 1993). The advantages of wake tracking may have promoted special adaptations in both hydrodynamic and olfactory receptor systems. One might expect specialisation in the lateral line system for analysing hydrodynamic details of the wakes (Engelmann et al., 2000) or chemosensory specialisation comparable to the forked tongues of snakes that facilitate tropotactic tracking of prey trails (Schwenk, 1994). These specialisations await further exploration.

3 The importance of the lateral line in nocturnal predation of piscivorous catfish

In a previous study we have shown that nocturnal piscivorous catfish track the wake left by a swimming prey fish to locate it. In a wake there are hydrodynamic as well as chemical signatures that both contain information on location and suitability of the prey. In order to determine how these two wake stimuli are utilised in prey tracking, we conducted experiments in which either the lateral line or external gustation was ablated. We found that a functional lateral line is indispensable to follow wakes of swimming prey. The frequency of attacks and captures was greatly diminished and the attacks occurred with considerable delay when the lateral line was ablated. In contrast, catfish with ablated external taste still followed the wakes of their prey prior to attacks. The external taste sense, which is solely responsible for finding stationary food sources, seems to play at most a minor role in the localisation of moving prey. Our finding adds an interesting new aspect to the ongoing discussion about the behavioural function of the lateral line in fish.

3.1 Introduction:

Trophic relationships have a major influence on activity patterns and sensory systems in fish (Dijkgraaf, 1933). Although sensory aspects of predator-prey interactions have been extensively studied in fish, the major focus has been on visual predators (Zaret, 1980). This is especially true for piscivorous fish (Hobson, 1979). Little is known about strategies and senses that non-visual aquatic piscivores use to detect and locate their prey . Information on fish activity at night is often inferred from static observation of their distribution or from analysis of stomach contents; most information comes from coral reefs where vision is still feasible at night (Helfman, 1993; Hobson et al., 1981). In temperate aquatic systems, however, vision is often limited due to turbidity and structures such as macrophytes. At night and at greater depths light is scarce and there are frequently conditions of total darkness. A few predatory fish have been specialising on these low-light niches where prey fish are less evasive and there is limited competition as well as risk from other visual predators. These nocturnal predators provide good models to investigate ecologically relevant non-visual interactions in fish. In a recent study we have found that European catfish (*Silurus glanis*) follow the wakes of piscine prey prior to attacking them in the absence of visible light (Pohlmann et al., 2001). In a wake there is hydrodynamic and chemical information about the sender that persists after the sender has moved on and thus considerably increases the “active space” in which the prey is detectable (Westerberg, 1990). Directional information in wakes and other plumes can be provided both by chemical and hydrodynamic gradients (Atema, 1996). The hydrodynamic information is estimated to be detectable in trail lengths in the dimension of several decimetres to meters and over several seconds, depending on flow conditions and the size of the fish (Bleckmann, 1993). The chemical directional information is present at least one order of magnitude longer, both in time and space (Westerberg, 1990). We found wakes as old as 10 seconds utilised and 2.5 cm long fish followed in distances of up to 40 cm for about 55 prey body lengths (Pohlmann et al., 2001). Wakes of moving animals are distinct flow patterns in which fine structure depends on the size, swimming velocity and the mode of swimming of their creator. The guppies (*Poecilia reticulata*) we used in our study swim in the push-and-coast mode, in which each tail beat creates a disturbance including a vortex ring, followed by a coast phase without fin movements dragging water behind (Breithaupt and Ayers, 1996; McCutchen, 1977; Müller et al., 2000). The height and the lateral distance between the vortices correspond to the size of the tail fin and thus of the fish. The specific structure of the wake provides information about swimming style. The sense of rotation and travelling direction of the vortices and the direction of the dragged water give information on swimming direction of the prey. A wake shows distinct structural changes when ageing (Hanke et al., 2000; Westerberg, 1990). Thus the hydrodynamic structure could inform a predator if the creator of the wake is suitable prey (size, swimming speed), in which direction it went and if the wake is fresh enough to be worth following (Bleckmann, 1993).

Fish can detect hydrodynamic structures with their lateral line organs (Kalmijn, 1988). These consist of free standing neuromasts and canal neuromasts that detect the velocity or acceleration components and the direction of water movements and are numerous enough on the body surface, especially the head region, to enable the detection and spatial resolution of fine scale structures (Herrick, 1901). The sensitivity of lateral line neuromasts covers the amplitude and frequency range found in wakes of small fish (Bleckmann, 1993; Bleckmann et al., 1991).

There is also chemical information in the wake. Substances are constantly and involuntarily released by all fish and are distributed with the water movements. Westerberg describes the evolution of a chemical trail in three stages: The initial mixing produced by a source, a stretching and deformation by the shear and a final stage in which molecular diffusion becomes important (Westerberg, 1990). In the wake there is incomplete mixing before the velocity fluctuations lose their momentum to viscosity. As the molecular diffusion of chemical substances is about 1000 times slower than the viscous dampening the remaining trail will contain small scale “frozen” filamentous and patchy structures of odour even after the hydrodynamic disturbance that have caused it is dampened out by viscosity. At the time the distinct hydrodynamic signature of a wake is lost the diameter of the chemical trail will be about 10 times larger than the source. With increasing age of the chemical trail molecular diffusion and shear will remove its distinct structure and dilute its concentration.

In a chemical trail a predator could use the degree to which small-scale concentration fluctuations have been smoothed out within the trail to determine the distance and direction to the source, independent of flow conditions (Atema, 1996; Westerberg, 1990).

Fish are known to have extraordinarily sensitive chemical senses enabling them to distinguish between different species and even individuals (Brown and Smith, 1994; Kleerekoper, 1969). Olfaction in fish is located exclusively in the nose, while gustation is perceived inside the mouth and in some fish also on parts of the body surface. In catfish there are high numbers of taste receptors on the whole body surface, with highest densities on the barbels and in the head region (Atema, 1971). For catfish gustation is the major chemical sense involved in foraging and feeding (Atema, 1971; Todd, 1971; Wunder, 1927). Bullheads (*Ictalurus natalis* and *I. nebulosus*) locate stationary food by their chemical sense alone using true gradient search (Bardach et al., 1967; Johnsen and Teeter, 1980); when locating dead meat the external taste sense is used exclusively (Atema, 1971).

In the present study we compared the foraging behaviour of catfish with ablated lateral lines or ablated external gustation to that of intact catfish to study the involvement of these senses in wake following. We used a video-based infra-red (IR) illuminated system allowing 3D evaluation of the animal behaviour with the exclusion of visible light.

3.2 Materials and Methods

3.2.1 Experimental techniques and protocol

In order to being able to observe fish behaviour in the dark by non-invasive means we used a glass tank (120 cm l x 60 cm w x filled to a height of 40 cm) that was illuminated by infrared back light. Interactions were recorded by IR-sensitive cameras from two directions on digital video (Sony GV-D 900E). The recordings of the two views were synchronised accurately to the frame.

Guppies (*Poecilia reticulata*) were chosen for their slow swimming behaviour and for their low tendency to thigmotactic (wall hugging) behaviour, minimising wall effects. They mostly use push-and-coast swimming, of which the hydrodynamics are well described (Müller et al., 2000; Videler et al., 1999). Guppies (total length 2.0 to 5.1 cm) were obtained from a local aquarium fish supplier. Four different catfish were used as predators, total lengths 20-31 cm. They were obtained from an aquaculture facility (Ahrenhorster Edelfisch, Badbergen, Germany) 7 weeks prior to the first trials and had been fed with live fish ever since to ensure their familiarity with living piscine prey. All fish were kept in holding tanks in the experimental room so they were subjected to the same temperature (18°C) and light regime (12:12 hrs light:dark cycle with 30 min lower light intensity periods at light changes). Catfish were kept individually in holding tanks and were returned to these tanks after each trial. Each individual catfish spent at least one day unfed in its holding tank between trials. Guppies were kept in one large holding tank in a group of about 100.

The experimental tank was cleaned and filled with aged, non-chlorinated tap water at ambient temperature before each trial, because catfish are known to deploy aggressive territorial behaviour to the chemical stimulus of another catfish (Todd et al., 1967). After the catfish was acclimated in the experimental tank for at least one hour in darkness each trial started with the introduction of a single guppy. For this, the investigator entered the experimental room through a double curtain to ensure total darkness and added one individual guppy with a small amount of water (< 50 ml) into the middle of the experimental tank. Five minutes after the prey had been consumed (viewed on monitors next door) the next guppy was added.

To avoid satiation a trial ended when 10 guppies had been eaten. A trial was aborted when the added prey fish was not consumed within 20 minutes. Thus, in each trial from 1 to 10 guppies could be consumed.

We ran 16 trials for each of three treatments: intact catfish (control), catfish with ablated lateral lines, and catfish with ablated external taste. Each trial consisted of the subsequent addition of 1 to 10 guppies, depending on the number of captures.

We compared the behavioural performance after the two ablations with the behaviour of the same fish before ablations. The control data were part of the data reported previously (Pohlmann et al., 2001).

3.2.2 Ablations

The ablation of the lateral line with $CoCl_2$ is reversible. We used the same four catfish as in the control trials. A single catfish was put into an incubation tank containing calcium-free artificial freshwater with 1 mM $CoCl_2$ (Karlsen and Sand, 1987). Calcium counteracts the effect of $CoCl_2$ by competitively displacing it. The artificial freshwater was made by adding stock solution (1.78 mM KCl, 3.57 mM KNO_3, 3.57 mM NaH_2PO_4, 7.14 mM $MgSO_4$ and 14.28 mM NaCl) to deionized water until the conductivity had reached 350 µS/cm matching the conductivity in the catfish holding tanks; NaOH was added to match the pH at 7.6 (modified after Karlsen and Sand, 1987). Catfish were kept in the cobalt chloride solution for 6 hours prior to transfer into the test tank filled with artificial calcium-free freshwater. The catfish was left to acclimate there for 1 hour prior to the start of a trial. The maximum time a catfish spent in the test tank was 3 hours, which is well within the time (over 24 hours) the total ablation of the lateral line persists in calcium-free water (Karlsen and Sand, 1987). To evaluate if lacking motivation was the reason that catfish did not attack prey in some trials, we offered those catfish a freshly sacrificed guppy directly in front of their mouth after each trial without captures. For data analysis only trials were included in which the catfish subsequently took this fish. To test for any effect of the artificial freshwater we ran one trial similar to the taste ablation trials but without $CoCl_2$ in the incubation tank. The feeding behaviour was similar to that of the control trials (data not shown).

The ablation of the external taste is invasive and irreversible. It was done two months after the end of the lateral line ablations. We only taste-ablated animals that had been used in the control and (reversible) lateral line ablation experiments to have comparable data in animals motivated to track. We removed the chemosensory area of the bilateral facial lobes in the dorsal medulla oblongata using the method developed earlier (Atema, 1971). This brain lesion was developed for a related species, *Ictalurus nebulosus,* where this external taste system is necessary to localise dead meat (non-moving, odorous food) and to trigger food pick up. It remains the only procedure to eliminate exclusively this one chemosensory system that guides the catfish's localisation behaviour for dead meat. The taste system of fish consists of two distinct parts. The one we ablated is innervated by the facial nerve (VII) subserving all taste buds on the body skin, lips, and anterior part of the mouth and ends in the facial lobe in the dorsal medulla oblongata. The other taste system contains all taste buds on the posterior part of the mouth and on the gill arches, innervated through nerves IX and X and ending in bilateral vagal lobes in the dorsal medulla oblongata. Vagal lobe ablation blocks swallowing, not locating behaviour.

We evaluated the success of the ablation after surgery and after every other trial by offering the catfish a piece of liver in the experimental tank. Liver was our catfish’s favourite food and intact fish show strong searching behaviour immediately after introduction of liver to the tank finding and consuming it within seconds. Catfish with ablated external taste, both *Ictalurus nebulosus* and *Silurus glanis*, took a long time to locate the food despite repeated chance contacts and close passes.

According to these criteria the taste ablation was successful in 2 of the 4 animals used earlier. By running 16 trials between both animals we ensured sufficient sample size.

Again, after each trial without attacks we put a freshly sacrificed guppy onto the catfish’s lips to evaluate hunger/motivation. In all these tests the guppy was immediately consumed.

3.2.3 Parameters and evaluation

We determined all attacks by reviewing the tapes of top and side view. Attacks consisted of successful captures and of snaps not leading to capture but directed at the guppy from a distance of less than 2 cm. Both of these show that the prey had been accurately localised by the predator. For each trial we recorded the time between introduction of prey and first attack and the time from introduction to capture (further referred to as “time-to-1st attack” and “time-to-capture”).

To determine differences across treatments in time-to-1st attack and in time-to-capture we used logistic regression analyses with posthoc contrast analyses for pairwise comparison (JMP 4.02).

From the video recordings we further determined if the guppy was moving prior to the attack. All attacks were categorised based on the video recordings as one of three types: 1) *wake following*: the predator swam along the same path as the prey, eventually attacking it; 2) *head-on encounters*: the predator encountered moving prey without prior path similarity; 3) *attacks on stationary guppies*.

In a previous study we have shown that our categorisation was justified by quantitatively analysing a sub-sample of the swim paths, calculating similarity indices between swim paths of predator and prey, and cross-validating our classification on the basis of these similarity indices (Pohlmann et al., 2001).

3.3 Results

We ran 16 trials for each of the three treatments (control, lateral line ablated, external taste ablated). In each trial 1-10 guppies were added sequentially, depending on the number of captures. In the control trials 74 prey fish elicited 99 attacks of which 65 were successful (see Table 3.1). Due to recording errors 5 attacks had to be excluded from further analysis. Of the analysed 94 attacks 55% were categorised as wake following and 30 % as head-on encounters. Only 19 (20 %) of all attacks were directed toward non-moving prey although prey fish were stationary 67 % of the time (averaged from 8 arbitrarily chosen sequences, total time 31 minutes).

Table 3.1: Attacks by treatment and category; summary of all trials.

Treatment	*Number of guppies added*	*Number of all attacks (number of captures)*	*% of attacks categorised as wake following*	*% of attacks categorised as Head-on encounters*	*% of attacks on stationary guppies*
Intact	72	99 (62)	55	30	15
Lateral line ablated	18	18 (3)	6	88	6
External taste ablated	56	67 (40)	27	58	15

In trials with lateral line ablations 18 guppies elicited 18 attacks of which only three were successful and only one attack (6 %) was directed toward a stationary guppy (see

Table 3.1). Almost all attacks (88 %) in the lateral line ablation trials were categorised as head-on encounters. The only attack categorised as path following occurred close to a wall and the path similarity was short and may have been incidental.

When the external taste was ablated 56 guppies elicited 67 attacks of which 40 were successful. In these trials 27 % of all attacks were categorised as wake following, 58 % as head on encounters and 15 % as attacks on stationary guppies.

The success rates (captures/all attacks) were similar in the control and the taste ablation trials (0.63 and 0.6, respectively), while it was much lower in the lateral line ablation trials (0.17). Contributing to the low success rate was the fact that catfish with lateral line ablation often attacked with delays. This hesitation allowed the guppy to escape from the approaching catfish, which then attacked the guppy's previous location. The percentage of wake following was highest in the control, intermediate in the taste ablation and lowest in the lateral line ablation trials (see Table 3.1).

Catfish with taste ablation, when following wakes, spent more time close to the guppies (within 2-4 cm) before attacking than intact animals. In the taste ablation trials there were an additional 12 sequences of wake following which did not lead to an attack. This was observed only twice in the control trials. Finally, only in the control and lateral line ablation trials did catfish show an enhanced interest (spending time and repeatedly returning) in places where the guppy had hung out recently.

Table 3.2: Time-to-1st attack and time-to-capture in each of the three treatments, given as medians and quantiles. Numbers in minutes, accurate to 1 sec. n gives the numbers of observations used for each calculation.

Parameter	*Control*	*Lateral line ablation*	*Taste ablation*
Time-to1st attack: median (25, 75 % quantiles) n	0.79 (0.33, 2.94), n=64	4.17 (1.4, 10.5), n=7	1.31 (0.59, 4.05), n=49
Time-to-capture: median (25, 75 % quantiles) n	0.87 (0.414, 3.242), n=58	4.17 (1.4, 17.7), n=3	1.23 (0.51, 4.21), n=40

In all three treatments stationary guppies were attacked less frequently than expected from the (high) percentage of time spent resting compared to time spent swimming.

Time-to- 1st attack and time-to-capture were shortest in the control and longest in the lateral line ablation trials (Table 3.2). When tested by logistic regression the time-to-1st attack was significantly shorter in the control than in both ablation trials (Table 3.3). The time-to-capture was significantly longer in the lateral line ablation trials than in the control and the taste ablation trials, but not different between control and taste ablations.

Note that in the lateral line ablation trials the number of observations was very low (Table 3.2).

Table 3.3: Significance values for differences in time-to-1st attack and time-to-capture comparing the three treatments. Separate logistic regressions for the two parameters followed by contrast analyses to determine differences between pairs of treatment. Overall significance values: p=0.0232 for time-to-1st attack and p=0.0355 for time-to-capture

Comparison	*Time-to-1st attack*	*Time-to-capture*
Control vs. Lat. Line Abl.	* (0.0341)	* (0.0127)
Control vs. Taste Abl.	* (0.0325)	Ns (0.3149)
Taste Abl. vs. Lat. Line Abl.	Ns (0.3147)	* (0.0376)

In all trials the catfish swam most of the time. In the lateral line ablation trials catfish showed a peculiar behaviour that was never observed in other trials: They were standing in the water without touching walls or bottom, undulating their long anal fin without changing their position for several minutes. This behaviour occurred in 8 of the 16 trials and for different duration (mean 28% of the trial time).

3.4 Discussion

Our results clearly show that the lateral line is indispensable for the ability of catfish to track the wakes of piscine prey and localise swimming fish, while external gustation is not. Catfish with dysfunctional lateral lines were unable to locate swimming prey by following their trails. The only instance in which corresponding swim paths preceded an attack by a catfish with an ablated lateral line was a short path overlap that occurred close to a wall. Hence the path similarity may well have been coincidental. The fact that catfish with ablated lateral lines showed considerably diminished frequencies of attack and capture points to the importance of hydrodynamic stimuli in all attack modes, not only in wake following. This is further supported by our finding that in all treatments stationary guppies, which only give weak hydrodynamic signals caused by their respiratory movements were attacked less often than expected from the total amount of time they spent resting. We do not exclude the possibility that internal gustation or olfaction were involved in the decision to follow a detected wake or to trigger an attack. But those senses alone did not suffice to follow wakes or readily attack prey, as shown by the lateral line ablation trials. The fact that lateral line ablated catfish readily consumed dead fish confirm findings by Enger *et al* that cobalt treatment does not noticeably reduce feeding motivation (Enger et al., 1989). Cobalt does not impair olfaction in the sub-lethal concentrations applied in this study (Brown et al., 1982).

External taste, on the other hand, does not seem to be mandatory for recognising and following wakes, since catfish with their external taste ablated failed to easily locate dead meat, but still showed a considerable percentage of wake following prior to attacks. The percentage of wake following here was lower than in the control, which might be explained by our observation that some wake following did not lead to attacks. If all 12 of those instances had led to attacks the percentage of wake following of 49.4 % would have been comparable to that of the control experiments. This and the observation that prey fish were attacked after a longer period of closely following the prey suggests that external gustation may trigger the actual attack as described for the pick-up response of non-moving food items in bullheads (Atema, 1971). Perhaps olfaction or internal taste, stimulated by odour entering the mouth cavity with the respiratory flow, supplemented the missing external taste before the final strike.

The physiological and morphological properties of the lateral line sensory system and its neuronal processing have been studied in detail (Bleckmann, 1993; Bleckmann, 1994). Sensitivity, frequency resolution and directionality have been investigated with artificial stimuli (mostly vibrating spheres). The biological significance of lateral line systems, however, can only be recognised by studying behaviour (Bleckmann, 1993). The lateral line system has been shown to be involved in many different behaviours such as detection and localisation of stationary objects (Abdel-Latif et al., 1990), obstacle entrainment and rheotaxis in fast flowing streams (Baker and C., 1999; Montgomery et al., 1997; Sutterlin and Waddy, 1975) and intraspecific communication such as schooling (Partridge and Pitcher, 1980; Pitcher et al., 1976) and mating (Satou et al., 1993; Satou et al., 1994). Lateral line involvement was also shown in different feeding behaviours of fish. Surface feeding by topminnows, *Aplocheilus lineatus* on struggling prey is mediated by the head lateral line (Bleckmann, 1980; Bleckmann and Schwartz, 1982). Here distance determination by lateral line analysis of water surface waves requires only one intact canal organ while determination of source direction depends on the spatial interaction of several organs (Bleckmann and Schwartz, 1982). The lateral line is further involved in detection and localisation of live zooplankton and crustaceans (Hoekstra and Janssen, 1985; Montgomery et al., 1995; Montgomery, 1989; Montgomery and Hamilton, 1997). Blinded sculpins, *Cottus bairdi*, consume live prey and react to other moving objects but ignore dead prey. Inactivation of the lateral line eliminates the feeding response to live prey (Hoekstra and Janssen, 1985). The spatial integrity of lateral line organs seems also necessary for correct directional response in the sculpin.

There are only two studies in which the involvement of the lateral line was tested in piscivorous fish, both using diurnal visual predators. Blinded pike, *Esox lucius*, which are visual ambush predators, attack live fish from distances of up to 10 cm only if their lateral line is intact (Wunder, 1927). Intact bluegills, *Lepomis macrochirus*, attack live fish in the absence of visible light when it is moving or after touch (Enger et al., 1989). When their lateral line is ablated they attack prey only after touch. We made similar observations with rather non-visual catfish.

Montgomery *et al* hypothesise that with deteriorating visual conditions the importance of lateral line cues increases (Montgomery et al., 1995). They report an observation on estuarine star-gazers, *Leptoscopus macropygus*, which initiated a strike in complete darkness when the front of the prey had just barely passed over the mouth without touch (Montgomery et al., 1995). This rapid strike mechanism is activated by lateral line input. They argue that the short range of the lateral line system is often seen as a disadvantage, but in terms of initiating a strike it does have the benefit of indicating the close proximity of the prey without the need for sophisticated central processing to determine target range. This is clearly different in the wake following we observed: here, catfish follow a series of past locations constituting the trail that leads to the prey, thus deriving directional information. Even in our spatially limited tank we found wake tracking over distances as long as 120 cm. Our study for the first time shows that fish adapted to conditions of limited visibility are utilising the lateral line to detect and follow the trails left by their prey. Using the hydrodynamic trail will considerably enhance the encounter probability under natural circumstances. Trail following was also reported for copepods following the trails of their mating partners (Doall et al., 1998). However, copepods were found to use chemical and not hydrodynamic cues in the wakes (Weissburg et al., 1998).

The observed peculiar swimming mode of catfish with ablated lateral line indicates that self-induced hydrodynamic stimuli may be important for monitoring the catfish's own locomotion in the absence of other cues (tactile, visual). The idea that the lateral line could be a locomotory proprioreceptor has been discarded because swimming movements of minnows did not appear altered after the lateral line nerve has been cut (Dijkgraaf, 1933). Roberts showed that the neuromasts of swimming dogfish discharge rhythmical bursts of impulses in a pattern which depends on the form of the locomotory movements (Roberts, 1972). The stimulus for this rhythm does not come from external water movements as it persisted when the fish performs swimming movements in air. The self-induced hydrodynamic stimuli are usually regarded as noise potentially interfering with the detection of biologically important cues (Montgomery and Bodznick, 1994). Our observations on swimming behaviour, however, suggest that in catfish self-induced hydrodynamic stimuli may contribute information on the animal's progress in the absence of other external stimuli. However, the fact that catfish swam normally most of the time shows that lateral line information is not essential for their swimming. Catfish swim by undulating only the anal ribbon fin not by undulating their body like dogfish or minnows. For this swimming style the detection of self-induced currents may be important. Only in blind cave fish self-induced currents were found to be used to gain information about its environment and detect obstacles (Abdel-Latif et al., 1990).

Our finding that nocturnal piscivores follow hydrodynamic cues in the wake of potential prey fish extends the classical definition of predation tactics in fish. Wake tracking can be categorised as stalking behaviour, which is normally referred to having a major visual component (Keenleyside, 1979).

Fish behaviour and predation strategies are very plastic and catfish can deploy a wide variety of strategies, depending on the environmental conditions and the nature of their prey. Wake following is not the only predatory strategy, as shown in our ablation experiments, but certainly important under natural conditions because being able to utilise wakes enhances the encounter rate of prey dramatically. Catfish are slow predators that have little chance to capture prey in light conditions when prey are aware of their approach (pers. obs.). Both *Silurus glanis* and *Ictalurus nebulosus* do not even respond to the visual presence of small goldfish in well-lit tanks but attack the prey when chemically or hydrodynamicly detecting their presence (pers. obs.). Thus searching for and tracking prey in the dark when the prey is visually less defended and approaching from behind where all sensory systems of the prey (e.g. lateral line, olfaction) are less likely to detect the predator's approach should improve capture success.

4 To see or not to see – predatory strategies of two nocturnal piscivors

Comparing the predatory behaviour of two nocturnal piscivorous fish in the absence of visual light showed two different strategies. Previous investigations indicated that food search of catfish (*Silurus glanis*) and burbot (*Lota lota*) is led by non-visual stimuli. We found that catfish were successfully capturing juvenile dace (*Leuciscus leuciscus*) in darkness following wakes to localise their prey while burbot rarely succeeded and did not utilise wakes. Because dace is not dominant in the burbot's natural diet we performed a second set of experiments with burbot and other prey species (juvenile perch *Perca fluviatilis*, ruffe *Gymnocephalus cernuus*, bream *Abramis brama*). The capture rate of these prey species was as low as that of dace. However, we found that perch were most frequently attacked. This may be due to its spatial preferences within the test tank that corresponded to that of burbot.

Morphological comparisons and behavioural observations lead to the conclusion that burbots are primarily visual predators of live piscine prey utilising even small amounts of residual light while catfish use non-visual cues. These results contradict earlier studies on burbot.

4.1 Introduction

Little is known about predatory strategies of nocturnal piscivorous fish. When light is scarce non-visual cues should become more important. Predators could use mechanical (hydrodynamic, acoustic, tactile) and chemical (gustatory and olfactory) cues of their prey. While tactile cues work only when the prey has actually been found and may trigger pick-up responses, hydrodynamic and chemical cues are found in the wakes of swimming prey and thus can be perceived in some distance of the prey. Chemical gradients are getting stronger close to resting prey and thus could also be utilised.

Catfish and burbot are both nocturnal and a substantial part of the diet of individuals larger than 25 cm, as used in this study, contains fish (Guthruf et al., 1990; Hartmann, 1977; McPhail, 1997; Mihalik, 1982; Omarov and Popova, 1985; Schultz, 1960; Vøllestad, 1992). Both species inhabit oligotrophic to eutrophic lakes and rivers. Burbots prefer colder temperatures and thus deep or alpine lakes and rivers, while catfish are often found in warmer, shallower eutrophic lakes.

In a previous study we were able to show that catfish (*Silurus glanis*) utilise the hydrodynamic trail left by swimming piscine prey to localise them (Pohlmann et al., 2001). This considerably enlarges the space in which prey is detectable. However, in that study we used guppies (*Poecilia reticulata*) as prey because of their slow swimming behaviour and large caudal fins that leave a strong hydrodynamic structure. We were able to show that in contrast to purely chemical gradient search for stationary food items (Bardach et al., 1967; Johnsen and Teeter, 1980) catfish do not orient exclusively by chemical information in wakes but utilise the hydrodynamic structures left by swimming prey (unpublished data). However, catfish and guppies are not sympatric. Thus in the present study we offered a sympatric prey species, dace (*Leuciscus leuciscus*).

In burbot (*Lota lota*) there is no detailed analysis of predatory strategies employed when capturing fish in the dark. There are, however, some findings from lab experiments indicating that burbots use non-visual stimuli of potential prey. Wunder (1927) performed multiple behavioural observations with intact, anosmic, or blinded burbots. He found that hydrodynamic stimuli initiate turning and following and in some instances even snapping behaviour in blinded or anosmic burbots and that chemical senses (olfaction and external gustation) are also strongly involved in feeding, while vision might supplement other senses but is dispensable. Teichmann (1954) compared the area of sensory olfactory epithelium and retina (normalised to body surface area) of multiple fish species. He found that burbots have exceptionally large olfactory epithelia with high densities of sensory cells while their eyes are rather small compared to other fish. Fish with large olfactory epithelia and small retinae are characterised as mostly crepuscular or nocturnal solitary predatory fish that hunt by olfactory cues. In feeding experiments with burbot under different light conditions they were found to successfully capture small cyprinids (belica, *Leucaspius delineatus*) in darkness or light intensities of 0.01 lux or less, while feeding rates on insect larvae (*Chironomus plumosus)* were similar under any illumination (Pavlov, 1959). These findings were due to the fact that under stronger illumination (0.1 lux) fish always escaped. Since both catfish and burbot are slow swimmers their nocturnal activity may reflect a niche were prey is less evasive.

Based on this information we analysed attack behaviour of catfish and burbot on juvenile dace, a sympatric prey species, in the absence of visible light. We paid special attention to the question if they utilise wakes of their prey, as observed for catfish attacking guppies.

Dace are rapid swimmers staying off the bottom even at night. Because burbot hardly captured any dace in the first set of trials we performed additional experiments with burbots and another 3 prey species that are part of the burbot's natural diet. Here we analysed spatial and temporal aspects of the swimming behaviour of the different prey species to investigate whether this gives rise to different susceptibilities to predation.

All results are discussed with respect to morphological and ecological traits of the predators.

4.2 Materials and Methods

In order to observe fish behaviour in the dark by non-invasive means we used a glass tank (120 cm l x 60 cm w x filled to a height of 40 cm) that was illuminated by infrared back light. Interactions were recorded by IR-sensitive cameras from two directions on digital video (Sony GV-D 900E), to obtain three-dimensional information. The infrared used was in the range 810-950 nm (maximum at 870 nm) which is outside the range of absorption of the visual pigments of fish (Dartnall, 1975). The recordings of the two views were synchronised accurately to the frame.

Four different burbot (total lengths 25-28 cm) and 100 dace (total lengths 4.0-5.9 cm) were caught in Lake Constance and kept in the lab for a minimum of two months prior to experiments to ensure good condition and habituation to aquaria and handling. Four different catfish (total lengths 20-29 cm) were obtained from an aquaculture facility (Ahrenhorster Edelfisch, Badbergen, Germany) four months prior to the trials. All predators had been fed with live fish ever since in the lab to ensure their familiarity with living piscine prey. All fish were kept in holding tanks in the experimental room so they were subjected to the same temperature as in the trials (18°C during catfish experiments and 15°C during burbot experiments) and light regime (12:12 hrs light:dark cycle with 30 min lower light intensity periods at light changes). Catfish and burbot were kept individually in holding tanks and were returned to these tanks after each trial. Each individual predator spent at least one day unfed in its holding tank between subsequent trials.

The experimental tank was cleaned and filled with aged non-chlorinated tap water at ambient temperature before each trial to remove any alarm substance from previous trials and because catfish are known to deploy aggressive territorial behaviour to the chemical stimulus of another catfish (Todd et al., 1967).

We ran 12 trials for catfish and burbot each. Each trial started after the predator had been acclimated in the experimental tank for at least one hour in darkness. The experimental room was entered through a double curtain to ensure total darkness and a group of four dace was added with a small amount of water into the middle of the experimental tank. A trial ended when all prey fish had been consumed or after 40 minutes.

A second set of experiments was performed in order to characterise the swimming behaviour of different prey fish species and resulting potential differences of predation success of burbots. We carried out 3 additional trials with each of the following species caught in Lake Constance: Eurasian perch (*Perca fluviatilis*, TL 3.6-4.5 cm), ruffe (*Gymnocephalus cernuus*; TL 3.8-4.6 cm) and bream *(Abramis brama*, TL 3.9-4.8 cm). All of these species are abundant in the littoral and sub-littoral zone of Lake Constance (Fischer and Eckmann, 1997; Pohlmann, 1995) where also burbot are observed to hunt at night; these prey species are part of the burbot's natural diet (Hartmann, 1977; Radke and Eckmann, 1996; Vøllestad, 1992). In each trial we again added four prey fish and trials were conducted as described above.

4.2.1 Behavioural parameters investigated

All attacks of all trials were evaluated from the video recordings. Attacks were defined as either captures or snaps; snaps are attack movements directed at prey fish from distances of 1.5 cm or less that did not lead to captures. We recorded the duration between the introduction of the prey fish and each attack accurately to the minute and the location of the attack (depth, wall). We categorised each attack as one of the following three types: head-on encounters (attacks on moving prey without prior path correspondence), wake tracking (attacks on moving prey with preceding path similarity), and attacks on stationary prey. The accuracy of this categorisation was confirmed earlier by numerical methods (Pohlmann et al., 2001). We further recorded instances of wake following that did not lead to attacks and counted close encounters that did not elicit snaps.

To characterise the swimming behaviour of the groups of different prey species we evaluated three arbitrarily chosen trials with burbot and dace and all three trials with each of the other three prey species. We recorded for one minute intervals whether the four fish were swimming along the walls (in ordinal values: 0=never; 1= some, i.e. the minority of fish, for short times; 2=most, i.e. the majority of fish, for most of the 1 min interval), their maximum, minimum, and mean depth, numbers of fish resting, and activity indices. For each minute the activity of this small group was categorised as: 1=slow (push-and-coast swimming with only one full tail beat between coast phases; 0.5-5 cm s^{-1}), 2=medium (push and cost swimming with more than one tail beat between coast phases, about 6-10 cm s^{-1}), or 3= fast (constant swimming without coast phase, above 18 cm s^{-1}). Due to the different swimming modes of the predators (fin undulation) their activity was categorised by velocity alone. To incorporate frequency of occurrence of these categories the predominant category was multiplied by 2 if another category was present as well and by 3 if it was the only category; absent categories were multiplied by 0. These products were added for each minute to express an ordinal measure of frequency-weighted activity index. A group of fish swimming predominantly with medium speed and sometimes fast would thus result in a value of 1*3+ 2*2+0*1=7. Activity indices were calculated only for the fish that were not resting. Medians were used to compare activity indices between different fish species. To compare behaviour of prey species we used a Friedman ANOVA and applied Bonferroni corrections, for all other comparisons chi^2 tests (all performed in Statistica for windows 4.5, StatSoft Inc. 1993).

4.3 Results

Catfish were clearly more successful than burbot in attacking (81 attacks in catfish vs. 49 in burbot; Chi^2 test: df=1, X^2=4.00, p=0.045) and capturing (43 vs. 8, respectively; Chi^2 test: df=1, X^2= 13.51, p=0.0002) juvenile dace (Table 4.1). The median number of attacks without capture per trial was 4 for burbot and 3 for catfish, while medians of captures per trial was 1 for burbot and 4 for catfish. Catfish almost always captured all four dace in less than 40 minutes while burbot mostly captured only one prey fish, never more than two (see Table 4.1 for trial durations). Hence the success rate (number of captures / number of all attacks) was significantly higher in catfish (0.53) than in burbot (0.15; Chi^2 test df=1, X^2= 8.22, p<0.0041).

Table 4.1: Summary of all attacks and captures of dace. Number of all attacks includes captures. Attacks and captures are summed over all 12 trials for each predator species. Times-to-capture and times-to-1st attack were measured (minutes) from the addition of the prey fish. Trial durations are maximally 40 minutes, after which trials were aborted. Durations of less than 40-min mean that all four prey had been consumed.

	Catfish	*Burbot*
Number of all attacks	81	49
Number of captures	43	8
Time (min) to 1st attack (median, max, min)	0.55, 4.64, 0.08	10, 33, 2
Time (min) to capture (median, max, min)	1.56, 4.64, 0.31	17.25, 40, 2
Duration (min) of trial (median, max, min)	15.39, 40, 5.87	40, 40, 40

Both catfish and burbot predominantly attacked moving prey (85% and 92 %, respectively). While catfish attacked most of the prey from the sides (38%) and behind (28%) and hardly ever from above or below, burbot predominantly attacked from below (35%) but rarely from above. Both predators attacked mostly near the walls of the test tank (Table 4.2). Catfish were frequently observed swimming free off walls and bottom, burbot spent almost all their time at the walls (Figure 4.1). Burbot captured most prey close to the surface (55%) or the ground (24%) and no attack took place both off the walls and ground. In contrast, 20% of the catfish's attacks occurred in the open water. Overall catfish attacked prey closer to the ground than burbot (Table 4.2).

Table 4.2: Percentage of all attacks on dace (absolute numbers given in parentheses) in each of the three categories and percentage of the different attack directions as well as percentage of all attacks occurring at the aquarium walls, calculated separately for each predator species. Further number of instances of wake tracking that did not lead to attacks.

	Catfish	Burbot
% wake tracking	16 % (13)	8.2 % (4)
% head-on encounters	69 % (56)	83.7 % (41)
% stationary prey	15 % (12)	8.2 % (4)
% at wall	80 %	98 %
Mean relative depth of attack (surface=0, bottom=1)	0.62	0.29
# tracking without attack	21	4

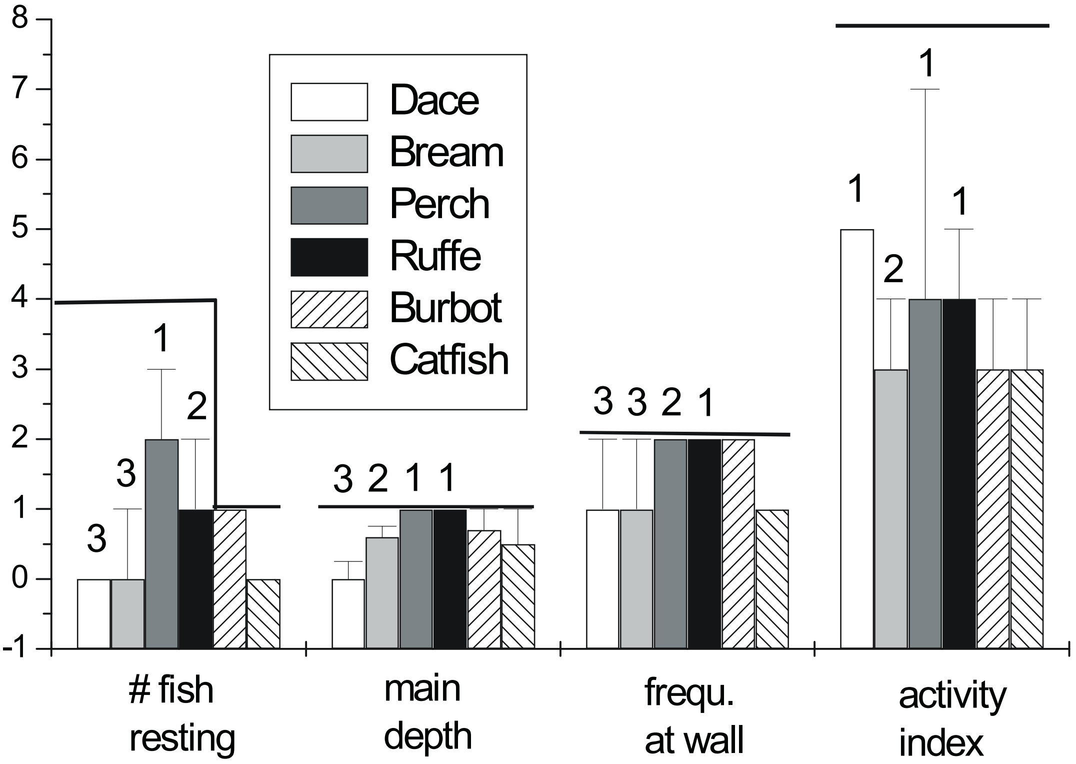

Figure 4.1: Spatial and temporal aspects of swimming in the absence of visual light comparing different prey fish with burbot and catfish. Medians (and 75 % quantiles as error bars) of the distributions of all one-minute intervals in three trial in the presence of a burbot. Dotted lines indicate maximal values possible for each parameter. Values below 0 are meaningless for all parameters and were only put in for visibility of the bars. Numbers above columns represent results from a non-parametric Friedman ANOVA (α=0.05) per parameter: significantly different species have different numbers. Depth is given in relative distance from the surface (=0, bottom =1), frequency at walls was recorded in three steps: 0=never, 1=sometimes/few during the interval, 2= most fish/throughout the whole interval. # fish resting gives the number of fish resting throughout most of the interval. For calculation of "activity index" see text “Materials and methods”.

The majority of attacks of both predator species were categorised as head-on encounters (Table 4.2). While in catfish there were 13 instances of wake tracking leading to attacks and 21 instances of tracking without attacks, burbots showed only 4 attacks preceded by wake tracking and 4 instances of tracking without attacks. The number of instances of wake tracking was significantly higher in catfish than in burbot (Chi^2 test df=1, X^2= 17.32 ,p<0.0001). In 12 of the catfish attacks categorised as head on encounters catfish adjusted their positions by turning and following their prey prior to striking but these pursuits were too short and the fish too close to be categorised as wake following. In burbot such turns were rare (2 observations) and never led to attacks. When intercepting wakes of dace that had swum less than 10 cm away catfish almost always (13 out of 15 wake encounters) reacted (i.e. changing direction or intensifying search in that place), while burbots only reacted to 4 out of 46 wake encounters.

The second set of experiments was performed to test whether burbot is more successful in attacking and capturing sympatric fish comprising major parts of its natural diet with swimming behaviour different from that of dace. Figure 4.1 shows the results of the observations on the activity index of burbot and catfish and different prey species (always groups of four individuals) in the presence of a burbot in darkness.

Burbots spent most of their time on the bottom or at the walls. They were rarely swimming off the walls and bottom at the same time: They were found at the walls in 93% of all intervals when off the ground (30% of total obs.). In contrast to catfish, which continuously swam throughout all trials, burbot rested about 50% of the time in intervals of up to six minutes. Catfish were frequently swimming freely through the water and often cruised at the surface for extended intervals.

Dace were swimming constantly and clearly faster than the two predators with the least variation in their activity indices, while bream showed a similar activity index as the two predators. Ruffe and perch were swimming mostly with slow to medium velocities. Perch activity index was the most variable in all species observed.

While dace were never resting and mostly swimming close to the surface, perch and ruffe were resting frequently and swimming close to the ground. Bream were hardly ever resting, swimming in mid water both off and close to the walls. Dace were also swimming both along the walls and through the whole tank, while perch and ruffe were observed mostly at the walls.

Perch were most often attacked by burbot. After unsuccessful attacks the attacked fish would show rapid escape movements for a short time. After that ruffe and perch usually settled down in another part of the test tank while dace would swim more slowly at the surface and bream would do either of the two.

Burbots attacked 13 times and captured 2 of the 12 added bream in the three trials. They attacked perch 19 times and ruffe 12 times and captured 1 and 2 of the 12 added fish, respectively. Again, burbot never captured more than 2 fish within the 40 minutes maximum trial duration. In our 3 arbitrarily chosen trials dace were attacked 10 times with 2 successful captures. The number of attacks and captures on all tested prey species were not significantly different (Chi^2 test, attacks: X^2= 3.53, p=0.32; captures:

X^2= 1.41, p=0.25). Therefore, the capture success of burbot was not higher with perch, ruffe, or bream than with dace.

4.4 Discussion

The comparison of catfish and burbot predation on dace clearly shows that under our experimental conditions catfish are the more successful predators. They attacked twice as often and captured 5 times as many prey as burbot. Further, they needed less time to attack and capture prey: Their total time in all 12 trials was 236 minutes as opposed to 480 minutes in burbot. Thus, given prey *ad libitum* and precluding satiation they might have attacked 4 times and captured 10 times as many prey fish as burbots within 480 minutes. The success of burbot attacking and capturing fish was not higher when offered sympatric fish other than dace.

In catfish we observed a substantial amount of wake tracking although less than observed before in a similar set-up with much slower swimming guppies (Pohlmann et al., 2001). Given the high swimming speed of dace it seems probable that while carefully following the hydrodynamic signals of wakes catfish were just too slow to actually come within striking distance of the prey. This is supported by two observations: catfish rarely encountered a fresh prey path without reacting to it and they frequently followed trails of prey without subsequent attack (21 out of 34 observed instances of wake following). These results show, however, that catfish employ wake tracking as a predatory strategy for locating sympatric, fast swimming and slender prey. This strategy is not restricted to capturing slow swimmers like guppies (Pohlmann et al., 2001). Catfish (*Silurus glanis* and *Ictalurus nebulosus)* do not respond to the visual presence of goldfish in well-lit tanks when maintained in the lab but attack the prey only when chemically or hydrodynamicly detecting their presence (personal observation of K. P. and J. Atema, Boston University Marine Program, MBL, Woods Hole, MA 02543, USA personal communication). Hence, in catfish the visual system does not appear to be important for catching prey.

In contrast to catfish, burbot followed prey paths only 8 times, four of which resulted in attacks. All but one of these took place when swimming parallel to walls and thus path similarities might have been coincidental. These low numbers and the observation of frequent prey trail interceptions without visible reactions suggest that burbot do not utilise trails left by potential prey.

Since dace are fast swimmers that do not contribute major parts to the burbot's diets we tested the attack and capture frequency of burbot on other prey species. Of all offered prey species perch were attacked most frequently (19 times). Comparing the behaviour and spatial distribution perch were resting significantly more than all other prey species and spending a lot of time at the walls and on the ground, where also burbots were mostly found. Thus the encounter probability between perch and burbot might have been higher than with all other prey species. The nocturnal distribution of juvenile fish found in Lake Constance resembles that in our trials: perch and ruffe are resting or slowly swimming close to the ground or structures while many cyprinids are swimming off the ground somewhere in the water column (personal SCUBA observations). Perch is often found to be the major prey fish in the burbot's natural diet (Guthruf et al., 1990; Hartmann, 1977; Schultz, 1960). This matches the high number of attacks on perch we observed in the lab and may be explained as a result of frequent encounters, frequent resting and a slow swimming speed which was comparable to that of the predator. To test these possible explanations we also counted instances of close encounters (prey came within 1 cm of the burbot) that did not lead to attacks or captures: Dace were encountered 11, bream 14, and ruffe 8 times while perch were encountered only twice. Thus, perch were almost always attacked when encountered. From our observations it was clear that dace and bream were swimming so fast that they were gone before the predator could position itself for the strike. This explains the high numbers of encounters without attack as well as the low numbers of attacks. The fact that ruffe were encountered and attacked considerably less than perch is explained by our observation that when a burbot came within 2-3 cm of a resting ruffe or encountering it head-on the latter would start swimming away and the burbot did not follow. It was found that the lateral line organ of ruffe is far more sensitive to hydrodynamic stimuli than that of perch (Disler and Smirnov, 1977), which may be an explanation for the different onset of escape behaviour. It seems that an approaching or attacking burbot is sensed earliest by ruffe thus preventing attack, but also in time by all other tested prey species to initiate a successful escape.

Burbot were previously reported to being able to capture piscine prey in complete darkness (Pavlov, 1959). Our findings and several observations made while maintaining burbot in the lab, however, indicate that they need at least a little residual light. In a room in which the only visible light source was an almost covered red LED at 3 m distance and facing away from the tank (the room seemed so dark that a human eye had to be dark adapted for 10 minutes before being able to perceive the light) a burbot tried to attack a juvenile dace through a glass wall that prevented any but visual cues. When adding small fish in dim light to holding tanks burbots would often rest until a prey entered their field of vision, follow them clearly with their eyes and then swim forward to capture them. In bright light they behaved similarly but their capture success was much lower than in dim light because prey fish were initiating escape movements before the actual strike. Similar observations were reported earlier (Pavlov, 1959). Under dim light burbot were well capable of consuming within 15 minutes 4 fish of the size utilised in our experiments.

Comparing our two predator species morphologically it is striking that catfish have very small eyes while those of burbot are comparatively large and very mobile. Large eyes are also common among nocturnal predatory reef fish (Helfman, 1993). The eyes of burbot are further equipped with a t*apetum lucidum*, which makes it more light sensitive. Burbots often inhabit clear waters. In Lake Constance there is enough stellar and lunar light in most nights at depths of 10-30 m even to the human eye where burbot are observed hunting in summer (personal SCUBA observations). Wunder (1927) observed that anosmic burbot swam directly towards a stationary food item 2 cm away and consumed it, while blinded burbot did not. He argued that vision can contribute to recognise food but is not the major sense involved. This view was further supported by Lehtonen (1998) who argues that burbots blinded by parasites show no reduced growth compared to visually unimpaired burbots. In contradiction to these earlier findings our data and observations clearly indicate an important function of burbot vision in capturing piscine prey. In the complete absence of visual light they have very low capture success and do not seem to utilise cues that extent the prey's body (e.g. hydrodynamic trails, chemical gradients). Furthermore, the relatively large eyes and their good capture performance under dim light conditions indicate the importance of vision for foraging in burbot.

Our results suggest that there are different foraging strategies of nocturnal piscivorous predators, employing either visual or non-visual cues. This has severe consequences on potential prey fish and may lead to predator-specific antipredator behaviour.

5 Creepy nights: alarm substance elicits anti-predator reactions of juvenile dace in darkness

Many cyprinid fishes possess specialised epidermal cells that release an alarm substance when ruptured. It has been repeatedly shown that released alarm substance elicits an innate fright response in conspecifics that serves to reduce the susceptibility to predation. It has been proposed that alarm substance enables potential prey fish to chemically assess predation risk, which is especially important in situations when visual information is inaccessible. In the present study we have for the first time analysed multiple aspects of the fright response elicited by alarm substance in the absence of visual light. We found that dace (Leuciscus leuciscus) showed distinct and significant changes in behaviour when exposed to alarm substance: decreased activity (measured as swimming velocity and the number of fish engaged in stereotypic movements or freezing) and a reduced vertical area use. The increased cover use and occasional dashing we observed as part of the fright reaction in light were absent in darkness. We discuss these findings with respect to the potential use in reducing predation risk at night.

5.1 Introduction

Many fish species in the superorder Ostariophysi posses chemical alarm substances that elicits specific fright responses. Von Frisch (1938; 1941) was the first to describe this and numerous studies have followed up on the characterisation of alarm reaction (for recent reviews see Chivers and Smith, 1998; Smith, 1992), the possible chemical nature (Brown and Smith, 1998; Pfeiffer et al., 1985) and evolutionary aspects (Chivers et al., 1996; Magurran et al., 1996; Mathis et al., 1995; Smith and Lemly, 1986). The alarm substance in most cyprinids is contained in specialised epidermal club cells and is released only when the skin of a fish is injured, e.g. by a predator. It further labels a predator who secretes alarm substance after ingesting a prey fish (Brown et al., 1995; Keefe, 1992; Mathis and Smith, 1993b). Released alarm substance thus informs other fish about an active predator nearby. Although alarm substance may elicit responses at day and night, the fright reactions have almost exclusively been studied under visual conditions so far. The induced reactions are innate and include the following behaviours which have been interpreted to reduce the susceptibility of the prey to visually orienting predators (Chivers et al., 1996): increased cover use, shoaling, reduction of activity (i.e. swimming speed, stereotypic movements, freezing), reduced area use (i.e. sinking to the ground) and dashing (rapid, erratic swimming which does not appear in each individual and mostly precedes schooling or reduced activity. For recent reviews see Chivers and Smith, 1998; Kats and Dill, 1998; Smith, 1992).

It has been argued that chemical alarm cues are especially useful when visual cues are unavailable, e.g. in structurally complex habitats, in turbid water or with cryptic or ambush predators and at night (Kats and Dill, 1998). However, only one study has included observations on alarm substance induced reactions in the absence of visible light (Jachner, 1995b). It reports the absence of an alarm reaction in darkness but considers only a few behavioural parameters. One would expect that nocturnal anti-predator behaviour differs from diurnal reactions as they may *not* primarily aim to reduce the visual conspicuousness. In temperate areas the hunting strategies of most nocturnal freshwater predators involve chemical and hydrodynamic cues that, unlike visual cues, do not radiate spherically from the source. In nocturnal predators (e.g. eel, burbot, catfish) the sense of olfaction (Teichmann, 1954; Teichmann, 1962) and/or gustation (Atema, 1971) dominates other sensory modalities (Teichmann, 1954). Chemical cues leaking from a prey are dispersed downstream by water currents. Predators may be guided to their prey by either the temporal/spatial distribution of chemical patches in the odour plume (Atema, 1996) or by the direction of the water currents carrying the odour (Kleerekoper, 1969). Swimming fish leave a wake behind that contains hydrodynamic and chemical cues. These cues in the wake persist for some time and can be detected by nearby predators. Our recent studies have shown that nocturnal predators (catfish) use the hydrodynamic and/or chemical cues in the wake to follow the prey along its three-dimensional swimming path (Pohlmann et al., 2001). Anti-predatory behaviours of fish in darkness should reflect these different search strategies of nocturnal predators.

The present study aims to address these issues. We use juvenile dace (*Leuciscus leuciscus*), agile freshwater cyprinids common to European temperate lakes and streams, that are under predation risk of several nocturnal predators (eels, burbot, catfish). We investigate the responses of groups of juvenile dace exposed to conspecific alarm substance and compare, describe, and quantify their alarm reactions in lab experiments in light and for the first time also in the absence of visible light. We hypothesise that in darkness behaviours that reduce the distribution of chemical cues originating from the potential prey and the amount of hydrodynamic disturbance should prevail in order to reduce predation risk to nocturnal predators.

5.2 Material and Methods

Juvenile dace (*Leuciscus leuciscus*) were collected from Lake Constance (Germany) and kept in the lab for more than 3 months. Prior to the experiments they were maintained in their test groups of 4 size matched individuals (TL 3.5-6 cm) for at least 2 weeks at 19°C on a 12:12 hour photoperiod and were fed chironomids every other day *ad libitum* and always on the morning of the experiment, because hungry fish show weaker fright reactions (Brown and Smith, 1996; Smith, 1981).

5.2.1 Stimulus preparation

The skin of 30 freshly sacrificed juvenile dace was homogenised, diluted in deionised water and filtered through paper filters. Total skin area collected from all donors was approximately 190.7 cm^2. Final concentration of alarm substance was 0.82 cm^2 skin ml^{-1}. 2.5 ml aliquots were frozen in separate Eppendorf tubes at –20°C until thawed immediately before each experiment. Lawrence and Smith (1989) tested the effect of different concentrations of alarm substance in minnows. Our final concentration of alarm substance in the test tank (0.006 cm^2 of skin l^{-1}) is well within the range of concentrations that elicited immediate fright reactions in fathead minnows (0.00017-0.017 cm^2 of skin l^{-1}). We did not add odour of a predator because we caught our fish in the wild and different previous experience may have led to differing behaviours. Learned predator recognition was reported to last for at least a year in fathead minnows (Chivers and Smith, 1994).

5.2.2 Experimental protocol

The test tank (120 x 60 cm and filled to 40 cm) contained aged non-chlorinated tap water and was carefully cleaned and refilled after each trial. Fish behaviour was documented using two digital video cameras from the side and above to enable subsequent three-dimensional analysis. Trials under light conditions were conducted under artificial room light, those in darkness used infrared back light. The test tank was equipped with a pump creating a modest flow to ensure a rapid distribution of alarm substance throughout the test tank. A silicon tubing was attached to this pump, delivering aged tap water throughout the whole experiment. Alarm substance was added into this tubing using a syringe. Dye visualisation showed that added substances were well distributed in the whole test tank 60 seconds after introduction. The tubing was replaced before each experiment. In the middle of the bottom of the test aquarium a cover was provided consisting of two horizontal dark PVC-sheets (Size 30*17 cm) on top of each other held 2 cm apart by four cylindrical PVC-legs.

A group of four juvenile dace was carefully transferred into the test aquarium to avoid release of alarm substance and given an acclimatisation time of 1 hour prior to the experiment under the same illumination as the actual experiment. We used groups of fish to monitor both group- and individual-based responses (Wisenden and Smith, 1998). At the start of each experiment fish behaviour was filmed for 15 min ("control"), after which 2 ml of alarm substance were added and fish behaviour was recorded for another 15 min interval ("treatment"). For adding the alarm substance, in dark experiments the room was entered through double curtains from an unlit corridor to ensure total darkness and in light experiments the person entering the room was visually isolated from the fish by black cloth. Eight groups of 4 dace were tested once under light and once under dark conditions each in random order. Groups were given two weeks between their two trials to avoid a weakening of the response due to habituation and because alarm substance was reported to alter behaviour for up to 6 days (Fricke, 1987).

5.2.3 Parameters

We analysed 10 min of behaviour immediately prior to the addition of alarm substance and 10 min immediately after its addition. Freezing, shoaling, reduced swimming activity, reduced area use and height above ground, dashing, and cover use are well known alarm reactions under light conditions for many species (Chivers et al., 1996). Many of them are reducing the predation risk (Mathis and Smith, 1993a) and visually transmit a warning to conspecifics. Therefore we analysed the following parameters from the video recordings with a temporal resolution of 1 sec:

Swimming speed: The velocity of each fish in one of four categories: resting (resting on the ground or hovering without forward movement), slow (push and coast swimming, 0.5-5 cm s^{-1}), medium (push and cost swimming with more than one tail beat between coast phases, about 6-10 cm s^{-1}), and fast (constant swimming without coast phase, above 18 cm s^{-1}).

Freezing: The number of fish resting in combination with ceasing any movement.

Dashing: The number of fish showing sudden darting movements with frequent changes in direction.

Stereotypic movements: The number of fish swimming in stereotypic movements perpendicular to a wall, heads at the glass.

Shoaling: The number of fish within one body length of each other.

Cover use: The number of fish inside the cover structure.

Depth: The position of each fish was recorded every 20 s to be in one of four horizontal layers (1 (bottom) to 4 (top layer)).

Swimming speed, freezing, dashing and stereotypic movements all represent different aspects of general activity that are closely linked but not equivalent.

5.2.4 Statistical analyses

The changes in all above listed parameters between the control and the treatment interval were tested separately for both illumination conditions in an exact logistical regression using SAS 8.1. Parameters that were interdependent (variance inflation factor >8) were tested separately. Medians of the distribution of each parameter were calculated for every 2 min interval and used in these analyses because data were linked through time series, individual fish react differently to alarm substances (Smith, 1992) and some reactions are short while others last longer. These medians were used as independent predictors, while the treatment (control vs. presence of alarm substance) was the dichotomous and therefore qualitative dependent variable. All analyses included group identity and number of previous alarm substance exposures as additional predictors to exclude biases due to these factors. This statistical approach was taken because our temporal resolution of 1 and 20 seconds (see above) is high and thus data points are interdependent. Using medians of 2 min intervals lowers the number of available data points considerably, however, therefore we applied exact logistic regressions that are suitable for low numbers of observations (Derr, 2001).

5.3 Results

Fish were behaving differently in light and darkness during the control intervals: The most obvious difference was that in light all four group members shoaled almost all the time and frequently inspected, but not used, the cover. In darkness they hardly ever were within one body length of each other and did not repeatedly swim near the cover. Under both illuminations they swam actively all the time, mostly showing stereotypic movements, but in darkness more slowly. Under both illuminations they used all four horizontal layers but were more often in the lower half of the tank. In darkness the frequency of visits to the upper layer was larger than in light.

The following statistical analysis was performed for all medians of all eight groups together, separately for each light condition.

5.3.1 Alarm reaction in light

Table 5.1 gives a summary of the number of groups changing their behaviour immediately upon addition of alarm substance. We calculated medians for the 2-min interval immediately after addition of alarm substance for each group and parameter and subtracted these from the corresponding medians of the 2-min interval just prior.

Table 5.1: Changes in behavioural parameters: Number of groups under light and dark conditions in which the median of the 2-min interval immediately after the addition of alarm substance decreased, increased or did not change in comparison to the median of the 2-min interval just prior to the addition of the alarm substance. Under both illumination 8 groups were tested.

		Velocity	Stereotypic Movements	Shoaling	Cover Use	Dashing	Freezing
Light	Decrease	7	6	1	0	0	1
	No Change	1	2	5	2	6	2
	Increase	0	0	2	6	2	5
Dark	Decrease	4	8	0	1	0	0
	No Change	3	0	8	6	8	2
	Increase	1	0	0	1	0	6

In light swimming velocity, the frequency of occurrence of stereotypic movements, freezing, and cover use changed significantly between the control interval and the presence of alarm substance (Figure 5.1 shows an example of one group, Table 5.1 summarises immediate changes of behaviour of all groups), as analysed by the medians of the distributions of these parameters for all 8 groups.

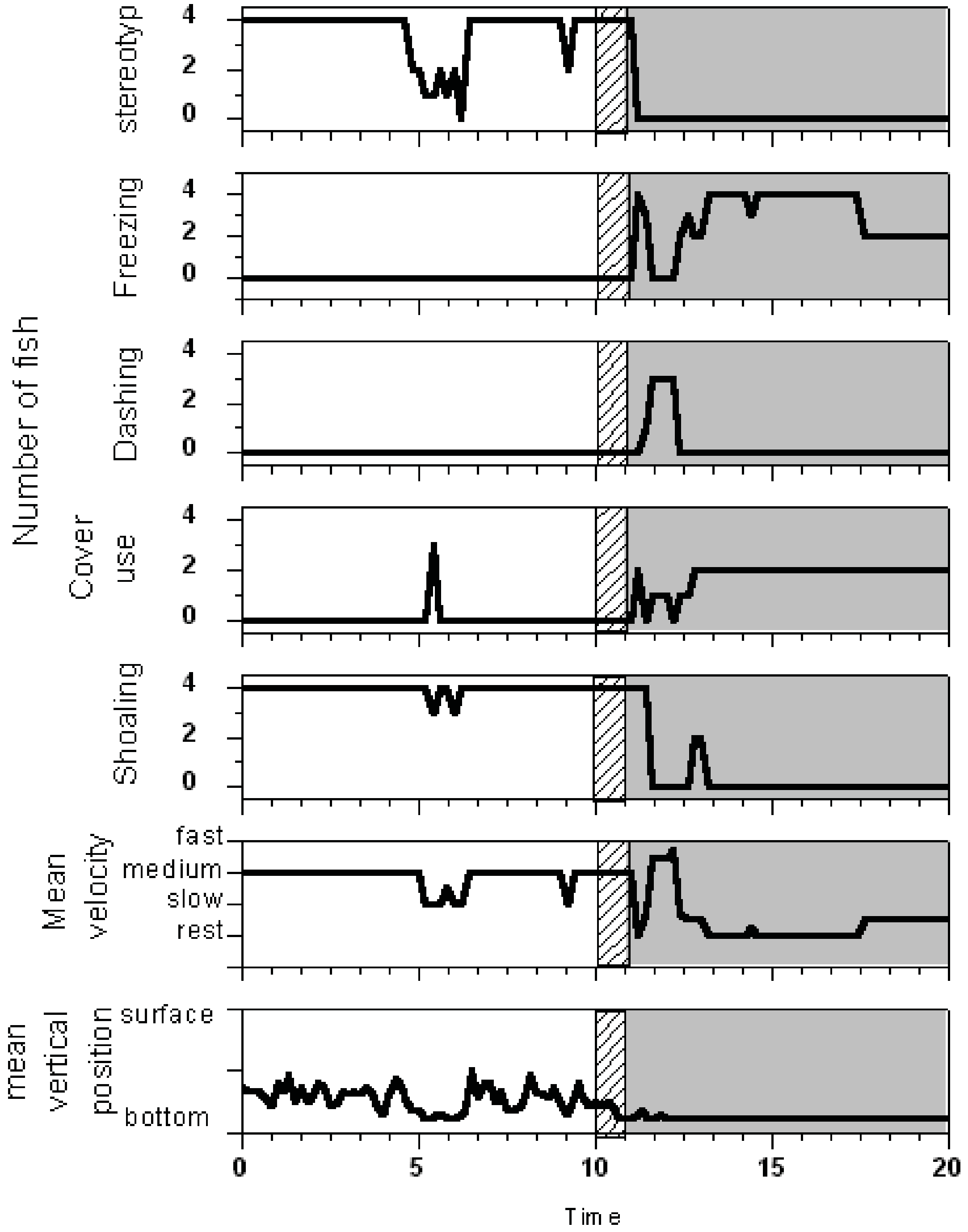

Figure 5.1: Fright reaction in light: example of the temporal development of all analysed parameters of one group of four juvenile dace in light. White: control interval, shaded: Alarm substance has been added but is not evenly distributed throughout the tank, grey: Alarm substance present throughout the tank.

The swimming velocity and the number of fish displaying stereotypic movements was significantly lower in the presence of alarm substance (p= 0.0005 and p=0.0029, respectively). The numbers of fish freezing and using the cover were significantly higher after the addition of alarm substance than before (p=0.0087 and p=0.0031) and fish were staying significantly closer to the bottom of the tank (p<0.0001). Dashing movements occurred only in 3 of the 8 experiments, exclusively in the presence of alarm substance and lasted very short. In the presence as well as in the absence of alarm substance all fish were schooling almost all the time.

5.3.2 Alarm reaction in darkness

In the absence of visual light general swimming activity was also reduced after addition of alarm substance (Figure 5.2 shows an example for one group, Table 5.1 summarises immediate changes of behaviour of all groups): The swimming velocity and the frequency of stereotypic movements were significantly reduced (p=0.0091 and p=0.0055) in the presence of alarm substance while the frequency of freezing was significantly higher (p=0.0074) and fish were significantly closer to the bottom of the tank (p=0.0003). Shoaling and cover use in darkness hardly ever occurred in the presence and absence of alarm substance and dashing was never observed (See Table 5.1).

In most trials the difference of behaviour was strongest in the first few minutes after addition of the alarm substance and decreased towards the end of the experiment. This decrease was more pronounced and started earlier in dark than in light (Figure 5.1 and 5.2).

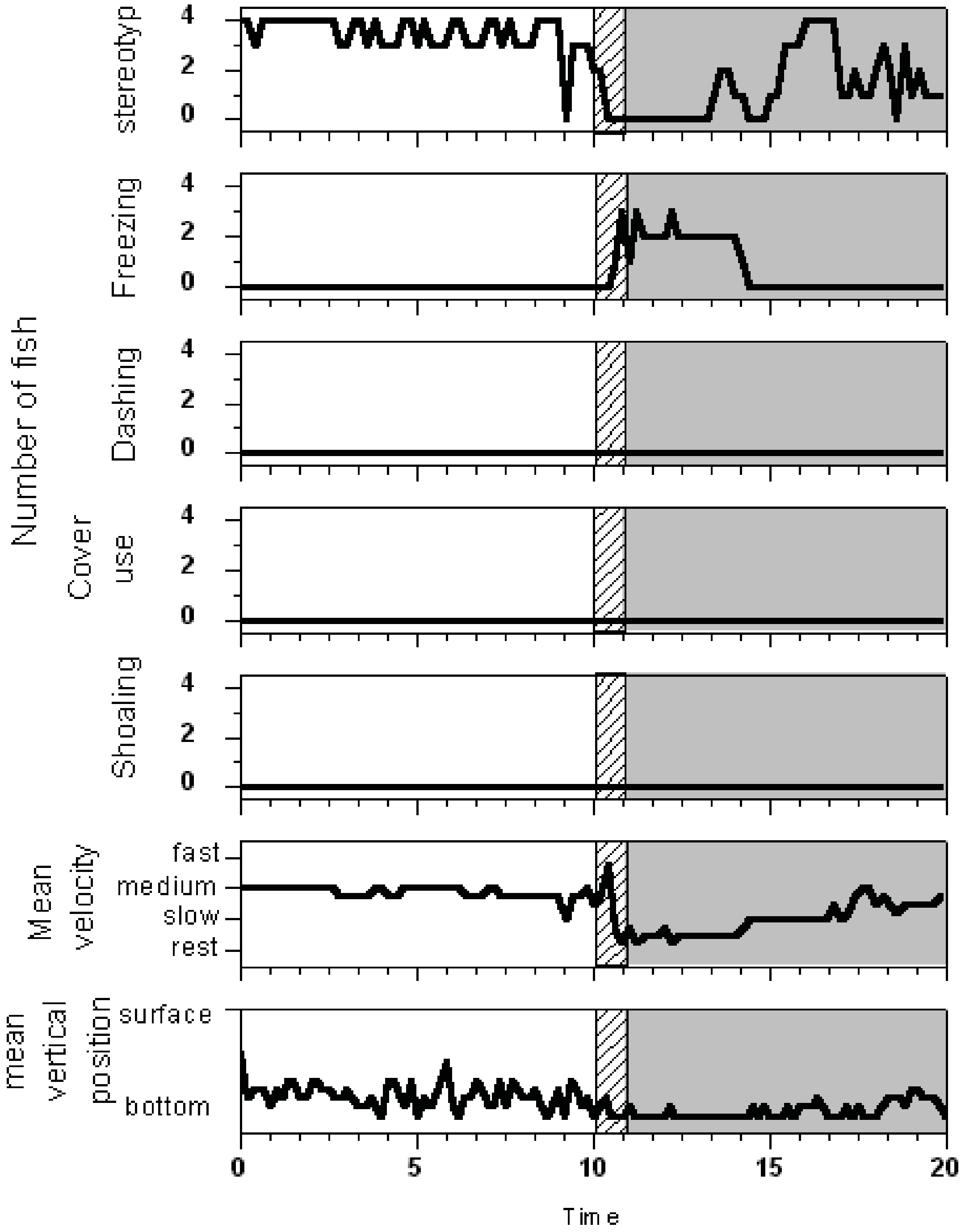

Figure 5.2: Fright reactions in darkness: example of the temporal development of all analysed parameters of one group under infrared illumination. White: control interval, shaded: Alarm substance has been added but is not evenly distributed throughout the tank, grey: Alarm substance present throughout the tank.

5.4 Discussion

Our results show that in the absence of visible light there are distinct and significant changes in behaviour when fish are exposed to alarm substance. The results confirm our expectation that fish exposed to alarm substance in the darkness reduce their overall activity. This is shown by a significant decrease in the swimming velocity and in the frequency of stereotypic movements and by a significant increase in the frequency of freezing (Table 5.1, Figure 5.2). Consistent with the responses of other cyprinids (reviewed in Kats and Dill, 1998) and with a qualitative study on dace (Schutz, 1956) the alarm responses of dace in light include an increase in cover use, dashing, and freezing and a decrease in swimming velocity and general activity (Table 5.1, Figure 5.1). This confirms that the extracted alarm substance was active and our fish responsive. In contrast to other studies we did not find increased shoaling. This was due to the fact that even before alarm substance was added all fish were schooling almost all time already, thus this parameter could not increase.

A previous study on the effect of alarm substance in darkness was not able to find any responses (Jachner, 1995b). This is due to the fact that they analysed only schooling and cover use, two behavioural aspects that are visually guided. We, too, found no changes in these parameters in darkness. Our study for the first time provides evidence that potential prey fish do react to alarm substance in the absence of light. It also demonstrates how they react. We will further discuss whether the reported alarm reactions are adaptive in reducing the probability to be captured by a nocturnal predator and consider the different trade-offs involved in diurnal and nocturnal responses.

Nocturnal predators in the absence of light can use chemical (olfactory or gustatory), mechanical (hydrodynamic, acoustic, and tactile) and in some cases (e.g. catfish) electric information to determine the presence, suitability, identity and exact location of potential prey. An anti-predator behaviour should thus minimise these cues and the space in which they can be detected.

Every fish is constantly and unintentionally releasing chemicals into the surrounding water. This cannot be completely avoided. These chemicals are distributed through water movements (molecular diffusion is negligible). There is nothing that a potential prey fish can do about ambient currents enlarging the space in which its presence and location can be chemically determined, except for avoiding areas with directional currents. If a fish swims through the water, however, it considerably extends the space in which the odour is detectable in the absence of strong currents (Atema, 1996;

Dusenbery, 1992). Hence the reduction of general activity and swimming velocity recorded in our experiments upon perception of alarm substance can be interpreted as adaptive with respect to nocturnal chemically searching predators.

In addition to spreading chemicals any movement of a fish leaves a specific hydrodynamic structure in the water that persists for some time and can be detected by a near-by predator through its lateral line system (Blickhan et al., 1992; Hanke et al., 2000). This structure holds information on swimming mode, velocity, location and size of the prey (Bleckmann et al., 1991; Hanke et al., 2000). In combination with the chemical information contained in the wake a potential predator could gain sufficient information to locate and capture a suitable prey. In a recent study we found that in darkness European catfish (*Silurus glanis*) predominantly prey on moving fish, mainly following the prey's wake, probably using the hydrodynamic and chemical information present in the wake (Pohlmann et al., 2001). Again, the reduction of activity decreases the probability of being captured as the prey is not perceivable to wake tracking predators when it remains motionless. The reduction of swimming activity also reduces possible acoustic swimming noise (Hawkins and Myrberg, 1983) of the prey detectable to the predator and decreases encounter probability with the predator.

The electric field of a small fish is present constantly and detectable by some catfish species of temperate areas in distances of up to 7 cm, depending on the size and sensitivity of the predator (Kalmijn, 1988). It is modulated by the breathing and excretion of the fish and is strongest around head and gills. Potential prey fish cannot avoid being detected by electroreception from small distances. However, immobility also reduces the detection space for electrical activity (Smith, 1997).

The decreased velocity and frequency of stereotypic movements as well as the increased freezing we found can thus serve as anti-predator behaviour under both illuminations. In light visual predators react strongly to movements (Godin, 1997) and motionless fish are less easily detected. In darkness, as explained above, decreased movement reduces the space in which a fish is detectable. When a fish freezes the only hydrodynamic stimuli are caused by its breathing and these are comparatively weak. A fish ceasing motion does not have to breath that rapidly. Furthermore, reduced swimming of potential prey reduces the encounter probability with slow swimming predators (Gerritsen and Strickler, 1977).

The changes in horizontal distribution in light can enhance the camouflage of potential prey fish. A fish sitting on a similarly coloured ground that has more disruptive structures than the water column is visually harder to detect. In the dark this does not hold up. We cannot think of an anti-predatory value of fish resting on the ground at night. In Lake Constance, from which the dace were collected, the nocturnal predators (burbot, eel and catfish) are benthic, swimming mostly on the ground with occasional excursions off the ground (pers. obs.). In this respect fish sitting on the ground do not have a reduced encounter probability. However, if dace cease swimming they sink to the ground. Thus, the decreased height in the water column may be just a result of the freezing without a specific adaptive value.

In darkness we did not observe any shoaling or cover use by the dace. Both of these behaviours are visually guided. The role of vision in shoaling has been studied in detail (Keenleyside, 1955, Hemmings, 1966 #231; Partridge and Pitcher, 1980) and it was found that shoals will disperse in the absence of light. It is well established that shoaling is an efficient anti-predatory behaviour during daylight (Magurran, 1990; Neill and Cullen, 1974; Wahl and Stein, 1988). A fish that joins a shoal of conspecifics benefits from anti-predator advantages such as dilution and confusion effects as well as the increased chance of detecting predators earlier and transmitting this information visually (Pitcher and Parrish, 1993). Although schools are more conspicuous, the advantages (safety in numbers, confusion effect, increased awareness) still overweigh. It has been shown that fish can school without vision (Pitcher et al., 1976). Helfmann explains the observation that fish do not school at night with the reduced incidence of predation and less need for predator-deterrent benefits of aggregating (Helfman, 1993). We think that schooling would even endanger fish in darkness since shoaling would lead to areas of increased chemical concentrations. This could attract predators towards the shoals from larger distances.

In darkness fish cannot see a cover. The dace may have detected the cover from close distance with their lateral line but they did not make use of it, although the cover was inaccessible to larger predators. Covers do not provide reduced conspicuousness to chemically or electrically guided predators as the chemical stimuli from the prey can leak out of and the electric stimuli radiate through the cover. This may have lead to a general loss of this antipredatory strategy in dace in the dark. Dashing is used to deter a visual predator (Smith, 1992). If prey fish are swimming rapidly and erratically a visual predator cannot foresee the direction of its next turn. In order to capture a prey it has to predict its location at the time it strikes. Furthermore, dashing similar to the stotting behaviour of gazelle visually signals to the predator the readiness of the prey to escape and warns nearby conspecifics (Zahavi, 1975). The probability of a successful attack is thus reduced and the predator might not even try. In darkness the location of a nearby predator is harder to detect and dashing increases the space and strength of hydrodynamic signals and might thus actually increase the prey's susceptibility. It also does not serve as a signal to predators or conspecifics over as larger distance when vision is limited. Fricke (Fricke, 1987) reported the absence of dashing in the fright reactions of blind cave fish and deduced that it is no longer functional in the non-visual environment of the cave.

In the absence of currents chemical alarm cues may persist even after the predator has left the area (Kats and Dill, 1998). This conservative effect of alarm substances is counterbalanced by a weakening of the response strength over time in extended exposure (Hemmings, 1966). We observed a clear difference in the duration of the observed fright reactions between light and darkness. In light the changes in behaviour upon addition of alarm substance lasted longer than in dark (compare Figure 5.1 and 5.2). This seems to be counterintuitive at first, because in light the costs involved in extended fright reactions are larger than in darkness. In light fish would have to cease feeding, defending their territories, or engage themselves in other social interactions (Brown and Smith, 1996; Ibrahim and Huntingford, 1989; Jachner, 1995a; Jachner and Janecki, 1999; Jones and Paszkowski, 1997; Lima and Dill, 1990; Milinski et al., 1997) while at night they mostly rest. Dace are visual feeders. Therefore one would expect a fright reaction at daytime to last shorter than during night. However, we did not feed the fish during our experiments to have comparable situations under both illuminations. Furthermore, in light the risk of being detected by a visual predator upon moving or upon leaving shelter may be higher than the risk of being detected by a chemically or hydrodynamicly searching predator since only visual but neither chemical nor hydrodynamic stimuli radiate spherically from the source and give an accurate and immediate image of the prey location. The prey, in turn, cannot visually assess the immediate location of the predator in the darkness. However, due to the ageing of hydrodynamic/chemical trails of the swimming predator the steepness of chemical gradients reveal information about the time elapsed since the predator was nearby (Atema, 1996; Hanke et al., 2000; Westerberg, 1990). By swimming around it can gather information about gradient steepness (Atema, 1996) and about immediate predation risk. Thus the early cessation of fright reactions in darkness does not necessarily reflect a decline in alertness.

Further complementary studies including the presence of nocturnal predators may reveal if the strategies used by dace in response to alarm substance in the darkness are effective in increasing their survival chance.

6 An automated radiotelemetry system to locate fish in 3D

6.1 Introduction

I was able to show that under laboratory conditions catfish utilise wakes of swimming prey fish to localise them while burbot probably need residual light to capture piscine prey, as described in the previous chapters. I further found that potential prey fish, upon perceiving the risk of predation through exposure to conspecific alarm substance, show characteristic changes in their behaviour that are suitable to reduce the risk of predation and can thus be termed antipredatory behaviour. In order to judge how relevant the observed predator and prey behaviours are and under which conditions they are exhibited one needs to study interactions in a larger and more naturally structured environment. It is difficult, though, to observe fish behaviour in the absence of visible light. Infrared illumination and video monitoring of behaviour is not feasible on a larger scale because infrared light is strongly absorbed in water. There is no method at hand to monitor fish swim paths in the necessary spatial (accuracy of a few cm) and temporary (1-2 seconds) resolution. Thus I developed a telemetry system that will enable future research of predator-prey interactions in the dark in a large and naturally structured environment.

6.2 Methods development

Our aim was to develop an automated 3D tracking system that would allow us to simultaneously obtain the positions of multiple fish in total darkness in a tank large enough to contain structures and provide different niches (e.g. a shallow and a deeper part). Since predator-prey interactions are fast the system needed to have a reasonable temporal resolution.

6.2.1 Hardware

The hardware restrictions were that the transmitters had to be small enough to be carried by and implanted into small prey fish and that battery life was sufficient to permit recovery from surgery and a few days of experiments.

To develop this method I used an outdoor tank 5 m long, 2.5 m wide, and 1.2 m deep. In order to simulate littoral conditions, I constructed a shallow area 20 cm in depth, a deep part 1.2 m in depth, both connected by ramp (see schematic drawing in Figure 6.1).

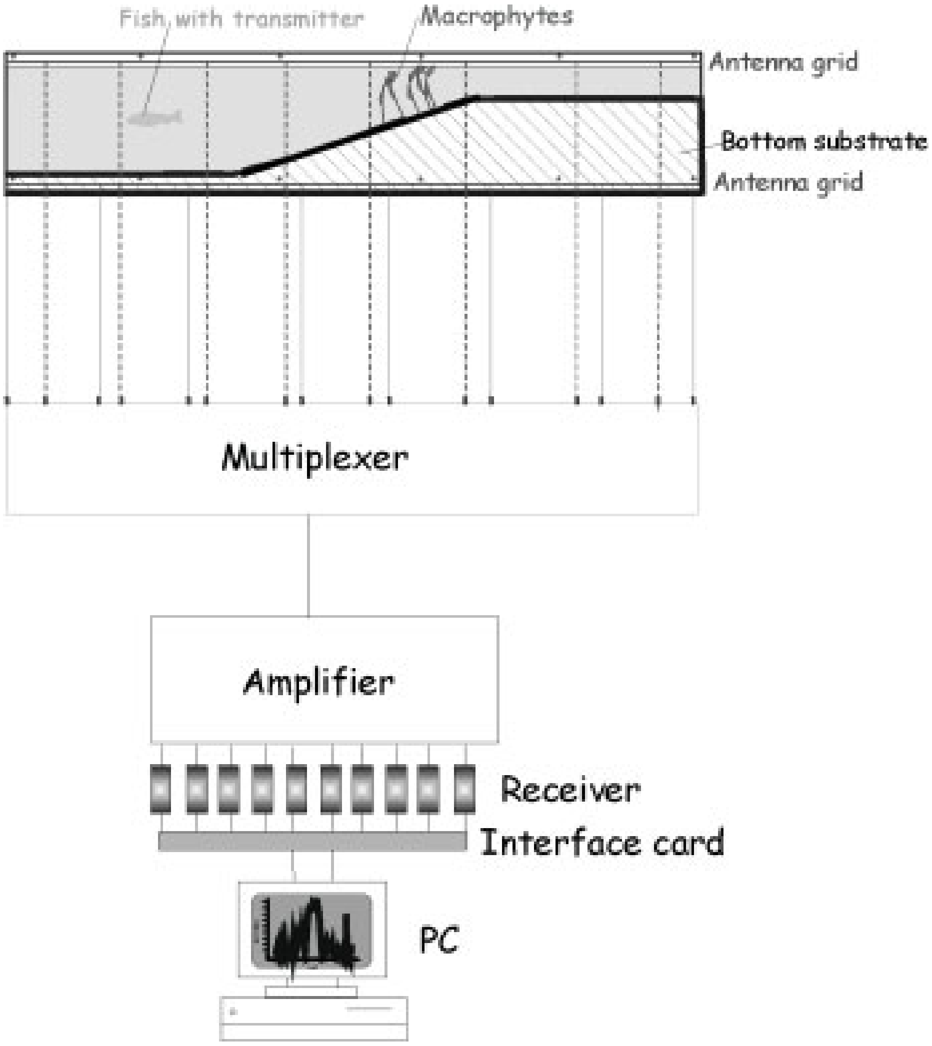

Figure 6.1: Schematic drawing of all components of the telemetry system

The implemented system consists of up to 10 miniature transmitters that operate on different frequencies and can thus be located individually. Their signals are received by an array of 14 or 16 antennae, each of which is individually connected to a single multiplexer (see Figure 6.1). The multiplexer scans all frequencies and delivers the signal to an amplifier that transmits peak signals in a sample-and-hold process to 10 receivers that are frequency specific, one for each transmitter. The analog signals of all 10 receivers are digitised by an interface card and stored on a PC in simultaneous real time for all 10 frequencies. The following describes all components of this system in more detail.

Figure 6.1 shows a schematic drawing of the experimental tank and the antenna array. Each antenna is an inductive loop (see Figure 6.3). The signal strength received depends on the radio frequency (RF) output power of the transmitter, the distance between the transmitter and each antenna, and the orientation of the transmitter.

Transmitter

A circuit diagram of the transmitter is given in Figure 6.2. We employed inductive transmission to avoid the necessity of a long transmission antenna. The transmitter contains an inductor while the receiving antennae are configured in loops, thus also acting as inductors.

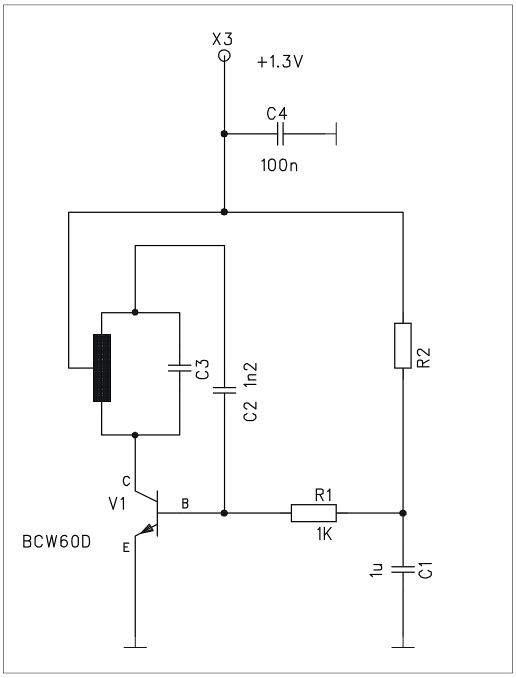

Figure 6.2: Circuit diagram of the transmitter. C=Capacitor, R=Resistor; V= Transistor; X= Battery, black box= Inductivity

The frequencies of the transmitters depend on their induction values, which correspond to different quality factors (Quality $Q \approx \sqrt{L/C}$ with L=inductivity and C=capacity) for the resonant circuit. The lower the frequency (large induction values), the higher the quality. With low frequencies the necessary initial voltage to initiate oscillation in the resonant circuit is small, which saves battery life. In addition, higher frequencies are attenuated in water, require long antennae, and have a strong frequency drift and hence would require a piezo for stabilisation. A piezo, however, is too large and heavy for our purposes. Thus the optimal frequencies determined and used were 1-3.6 MHz, which is in the long wave range used for instance in submarine communication. Different frequencies were achieved by employing different sized inductors in the transmitters. We used a Varta chron V393 battery that met the following requirements: it has an operating temperature of –10° to +65° C, weighs only 1.08 g, is comparatively small (0.24 cm^3) and has a stable voltage output of 1.55 V (0.01 V scatter) for over 95% of its life time. We pulsed the output signal of the transmitters to maximise the battery life time, transmitting 10 ms pulses with pause intervals of 70-107 ms. The length of the pause depends on the battery's operating voltage. Because batteries discharge when overheated, we spot welded a connection pin to the batteries. This process causes only a very short and minute heating of the battery, in contrast to conventional soldering or welding. The pin was then connected to the transmitter set-up. When reproducing signals with different batteries, deviations in the receiver signals were 2-13 % (largest deviations with smallest signal frequencies). The signal strengths varied 9-11% over 5 hours at 20°C. The temperature dependent frequency drift was 40 kHz for the highest frequency (3.6 MHz) and zero drift for the lowest frequency (1 MHz) transmitter in temperature shifts from 0 to 20 °C.

To reduce temperature effects, protect transmitters, and prevent condensation, the transmitter was coated with insulation spray (Plastik 70 Schutzlack, KontaktChemie) and, after connecting the battery, coated with a layer of bee's wax and paraffin before implantation. The coated transmitters have a volume of 2.2 cm^3 and a mass of 2.47 g, resulting in an under water mass of 0.37 g. I found that they can be carried by prey fish (perch) of 9 cm length when implanted into their abdominal cavity without noticeably changing their swimming ability. Two burbots (total length 30 and 32 cm) were each fed a transmitter embedded in bait. They retained the transmitter for more than 2 weeks in their guts, consuming 3 to 5 juvenile fish daily. They remained in good health and did not show any behavioural changes as compared to before.

Antenna array

The antenna array had 2 identical antenna layers consisting of multiple antenna loops each, one set above the water surface and the other one below the bottom substrate of the test tank that was 5 * 2.5 m with a depth of 1.2 m.

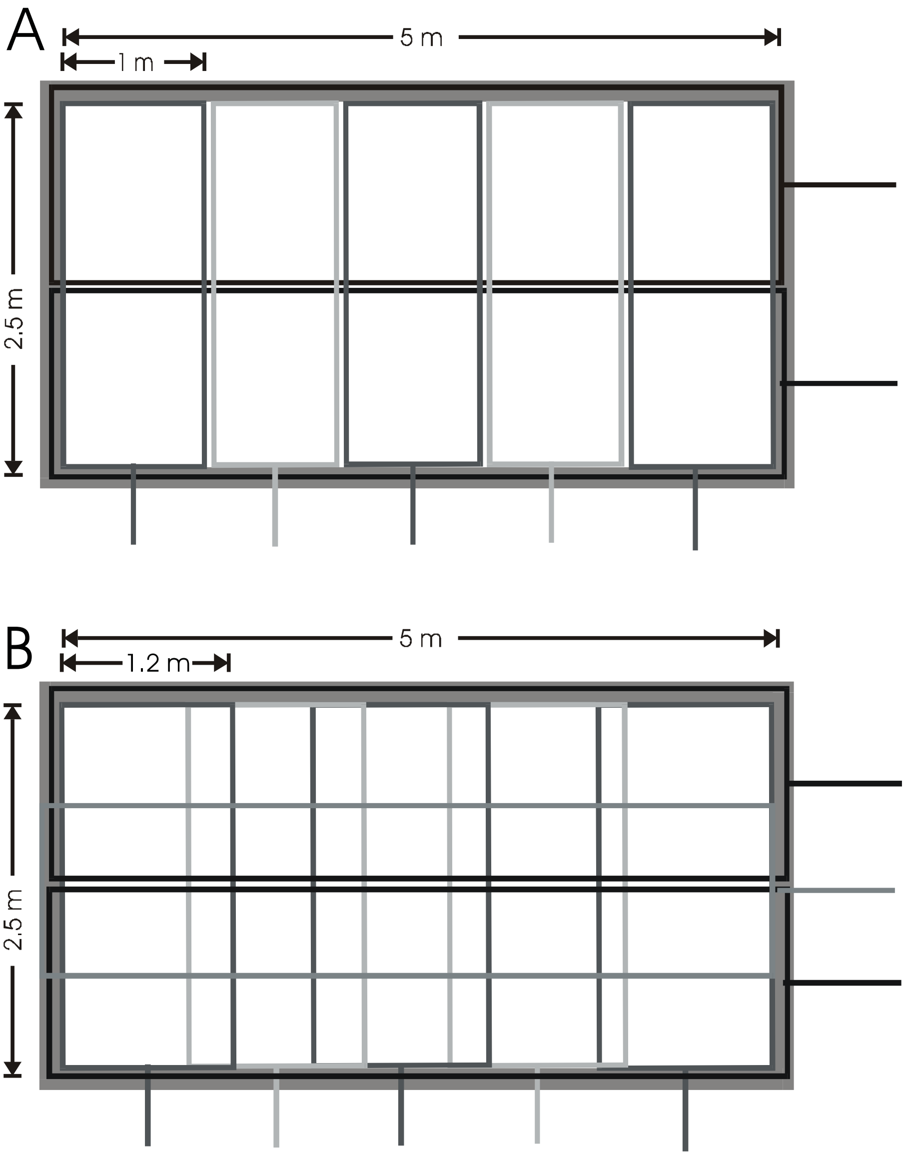

Figure 6.3: Schematic drawing of the two different antenna arrays. Since the layers on top and bottom of the test tank were identical, only one layer of each array is depicted. Each square represents a different antenna loop. **A**: array 1 with 7 (total 14) antennae, adjacently set; **B**: array 2 with 8 (16) antennae, overlapping design.

I tested 2 different arrays as depicted in Figure 6.3. Array 1 consisted of 14 antennae: 5 spanning the whole width of the tank and set up on different length sections, and 2 spanning the length and half the width of the tank each. These layers of 7 antennae were set up twice, one above the surface and one below the ground of the tests tank. The antennae covering the width (further called “length antennae”, because they were essential to predict the position in the length axis of the tank) were 1*2.5 m squares, those covering the length (“width antennae”) were 5*1.25 m squares. They were flanking each other (see Figure 6.3 A). Array 2 consisted of 16 antennae, 5 for length and 3 for width in each layer. They were overlapping (see Figure 6.3 B), length antennae consisting of squares of 1.2*2.5 m and width antennae of 5*1.25 m.

Signal sampling

The multiplexer connects to all of the individual reception antennae, sampling the complete frequency spectrum. The multiplexer's sample period of 130 ms guaranteed the reception of at least one, usually two, signal pulses from each transmitter. An amplifier was needed on the multiplexer output in order to step up the 50 Ω impedance of the whole spectrum to 50 Ω impedance for each receiver. Each receiver consists of a narrow-band filter; the detection range of each filter was selected to receive a signal from only one particular transmitter and to allow for frequency drift (see above). The receivers stored the peak value of each 130 ms interval in a sample and hold mode. A PC connected through a synchronous analog-to-digital interface card controlled the sample and hold mode. To reduce interference, the interface card and PC were connected by two fibre optic cables. Signals from all transmitters were sampled every 2 seconds.

6.1.2 Calibration

I calibrated each of the two antenna arrays separately by recording values for three different transmitters on a 10 *10 *10 cm grid throughout the tank. These data were used to develop algorithms to predict the location of the transmitter from the signals received by all antennae.

6.3 Algorithms for 3D position calculation

6.3.1 Smoothing of calibration data

Short-term interference from radio transmissions or electric devices are to be expected in the long wave range. They add up onto the real signals. I smoothed the calibration data in order to minimise the interference errors and to obtain the most reliable calibration. I applied two different approaches: local regression and Fourier transformation. For the Fourier transformation I determined all Fourier frequencies and used the lower third of the spectra to predict the signals received by each antenna in every point of the calibration matrix, thus smoothing (low pass filtering) the signals. The local regression smoothing was done by taking the received signal strength at each calibration point within a 21 cm radius off the position to be smoothed and weighing them using a Epinechinikow kernel, thus reducing their influence on the smoothing with increasing distance. Signal strengths were multiplied by this weight, added and divided by the number of used points. This was done for each position in the calibration matrix. Both smoothing methods were performed in SAS 8.0.

6.3.2 Predicting positions

The signal strengths at the calibrated positions were used to predict unknown positions from the received signal strengths of all antennae by two different methods. To obtain a measure of error I first predicted calibrated positions and compared the results to the actually calibrated positions. Once the accuracy in the prediction was good enough, a further essential step was to predict positions from antennae values that were not part of the calibration matrix but the positions need to be known to determine accuracy also between calibrated points. If the accuracy again is as desired one can move on to predicting unknown locations, e.g. paths of swimming fish.

Regression model

The smoothed as well as the original data served as predictors in a general linear model procedure to predict the location of the transmitter. I introduced non-linear elements by including interactions between predictors into this model.

Residuals were calculated as differences between each calibrated location and that predicted by the regression model. Their distribution was used as a criterion to optimise the algorithm. I predicted length, width and depth separately to avoid error propagation. All calculations and analysis were performed in SAS 8.0. For determining the location in the length dimension of the tank I used the values received by all antennae (signal strengths received by an antenna are further referred to as “antenna values”) as linear elements and additionally all interactions between the length antennae values within one layer; for the prognosis of width all antennae values as linear elements and interactions of the width antennae values; for the determination of depth all antennae values and the interaction of each pair of antennae values that held identical positions in the upper and lower layer of the antenna array. The inclusion of squared or higher order antennae values did not improve predictions in any of the dimensions and was thus omitted.

I found systematic difficulties to predict certain locations in the test tank with the first antenna array. I simulated a different antennae set-up and yielded better prediction results. Thus I changed the spatial antennae configuration (array 2) and calibrated the system again. Since the results were better but still not as accurate as needed I applied a different approach by utilising a neuronal network back-propagation algorithm.

Neuronal network algorithm

Artificial Neural Networks (ANNs) are an abstract simulation of a real nervous system that contains a collection of neurone units communicating with each other via axon connections. Such a model bears a strong resemblance to axons and dendrites in a nervous system.

General features of neuronal networks

There are two phases in neural information processing. They are the *learning phase* and the *retrieving phase*. In the learning phase, a training data set is used to determine the weight parameters that define the neural model. This trained neural model will be used later in the retrieving phase to process real test patterns and yield classification results.

An artificial neuronal network consists of a layer of input units (the predictors, all antennae values) and their biases (setting the “activation level” above which an input node contributes to the output), connected by a layer of hidden nodes to an output layer that receives the predicted values (here the predicted positions of the transmitter). Figure 6.4 gives a schematic representation of this structure.

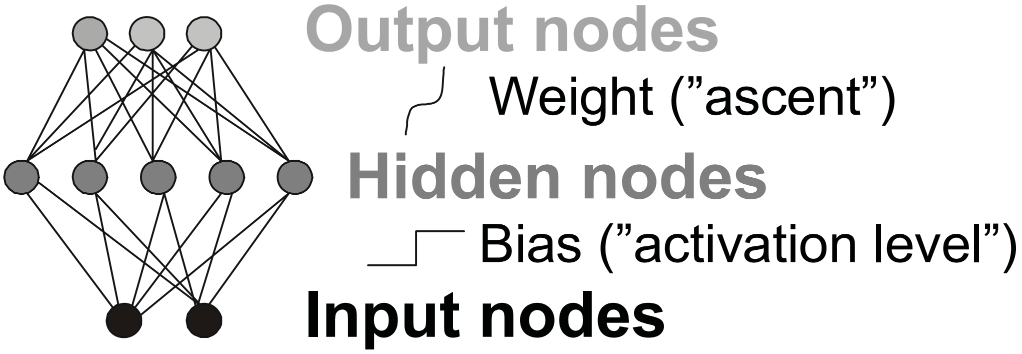

Figure 6.4 : Schematic representation of a general 2-layered neuronal network.

There are as many input nodes as there are predictor variables, as many hidden nodes as necessary for the complexity of the function that needs fitting, and as many output nodes as there are dependent variables.

In each hidden node weights are chosen for each input variable. Each hidden node acts as a filter by computing a certain *activation function* of the weighted sum of its inputs. We used the S-shaped hyperbolic tangent (tanh) function as the activation function. Theoretical results indicate that given enough hidden units, a network like the one we used here can approximate any reasonable function to any required degree of accuracy. In other words, any function can be expressed as a linear combination of tanh functions:

tanh is a *universal basis function*. Because of the shape of the tanh function, input data have to be centred (by subtracting the mean) and normalised (by dividing by the standard deviation) before being weighted. The bias shifts the tanh curve along the x-axis (determining the intercept, thus setting the "activation level" above which an input node contributes to the output, analogous to a neurone that starts firing) and the weight determines the ascent of the curve.

In the initial step there is a random combination of weights chosen for each input variable in each hidden node. We used a feedforward network trained by back propagation of error with 20 hidden nodes. The output is then compared through a backpropagation algorithm with the actual measured position of all calibrated points. The weights are modified in each further step, the sum of mean square errors between output and original positions is calculated through back propagation again and the weights are again modified accordingly in the next step to further reduce the sum of mean square errors. This is repeated in every learn step. After the predictions are sufficiently accurate (learning phase), the optimised combination of weights is applied to the test data that do not have known results (signals from swimming fish; retrieving phase).

In programming this neuronal network algorithm we followed the instructions given in http://www.willamette.edu/~gorr/classes/cs449/intro.html with some specific modifications.

Specifics of the applied network algorithm

To reduce the number of necessary learn steps I calculated 100 initial steps with random weights and chose the one with the smallest error to start the learning process. The link function of the hidden and the output layer I used was a logistic function, because the solutions are restricted to the dimensions of our test tank. I used steepest ascent as the optimisation technique.

I accumulated the gradient contributions for all data points in the training set before updating the weights. This method is often referred to *as batch learning*. We chose this method over the often recommended online learning method because there is a fixed training set (no new data are coming in since only one calibration of the whole tank is done), there is no redundant information in the training set (each position was only measured once in the calibration grid) and the calibration is a stationary environment (the data do not shift systematically over time). With the given application batch learning in clearly faster than inline learning. I included cross validation to avoid overtraining.

6.4 Results

6.4.1 Signal structure and smoothing

In order to visualise the signals received by a fish that would swim through the tank signal strengths from calibration positions 20 cm below the surface and 50 cm off a side wall along the entire length axis of the tank are plotted (Figure 6.7, for clarity purposes this figure shows only signals of 2 adjacent antennae). In array 1 (Figures 6.7 B1) I found that the closer the transmitter was to the antenna wire, the weaker the received signal was. Antennae immediately adjacent to each other have weak signals in the same positions. Because information is scarce and ambiguous in these areas, thus giving rise to large errors in the determination of positions, I chose to design antenna array 2. Overlapping antennae should have their weakest signals in different positions. However, due to induction between antennae the peaks shifted from the middle of the loops to under the wires, resulting in new areas where all signals are weak (Figure 6.7 B2).

The original data do not show any apparent interference (6.7 B1 + B2) and smoothing the data in array 2 changed the values considerably (Figure 6.7 C2 + D2 as compared to 6.7 B2). I thus performed subsequent analysis also with the original not smoothed data.

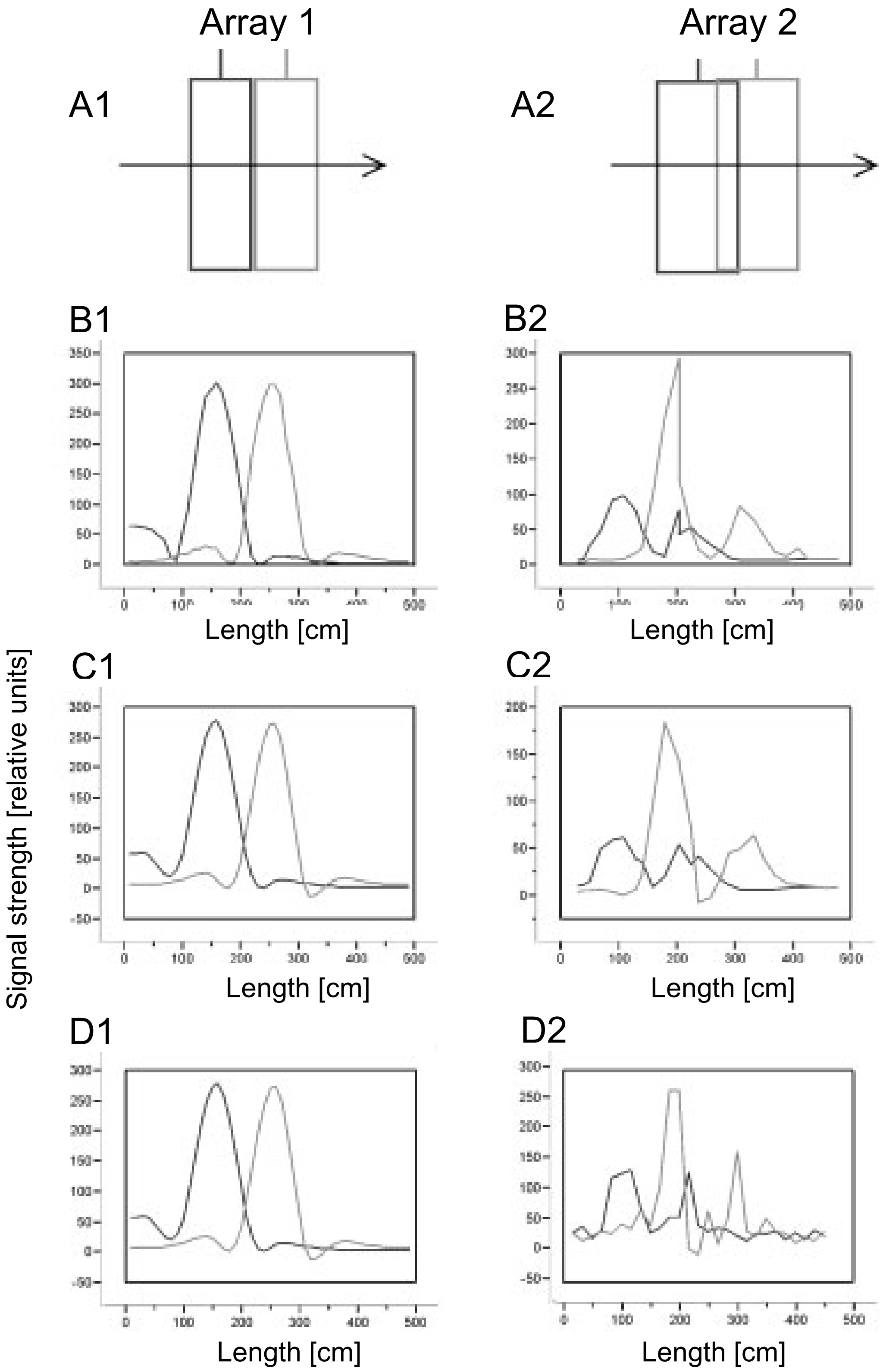

Figure 6.7: Received signal strengths of two adjacent length antennae of the bottom layer resulting from a calibration points along the entire length axis of the tank 20 cm below the surface and at a width of 50 cm. **Left panels** (number**1**) = antenna array 1, **right panels** (number **2**) = antenna array 2. Panel **A**: spatial set-up of the antennae depicted in relation to the signal strength. Panel **B**: non smoothed signal strengths, Panel **C**: signal strengths smoothed by local regression, Panel **D**: signal strengths smoothed by Fourier transformation. x-axis: positions of the length axis in cm, y-axis: received signal strengths in relative units.

6.4.2 Prediction

To determine the reliability of prediction I calculated the distribution of all residuals of data points in the calibration data sets. Residuals were derived by subtracting the predicted position separately in all three dimensions from each calibrated position. Because residuals did not show normal distribution in some cases I calculated the mean residual and the 25% and 75% quantiles of the distribution, which are shown in Figure 6.8. All medians (depicted by the diamond symbol) were close to zero, which means distributions were not skewed, i.e. the error was similar in both directions around a given position. Each horizontal bar in Figure 6.8 depicts the range (in cm) in which 50% of all errors were. The longer it is, the larger the errors fell. Since the tank dimensions and thus the possible errors were different in all directions it is understandable that errors in depth are smallest in most cases.

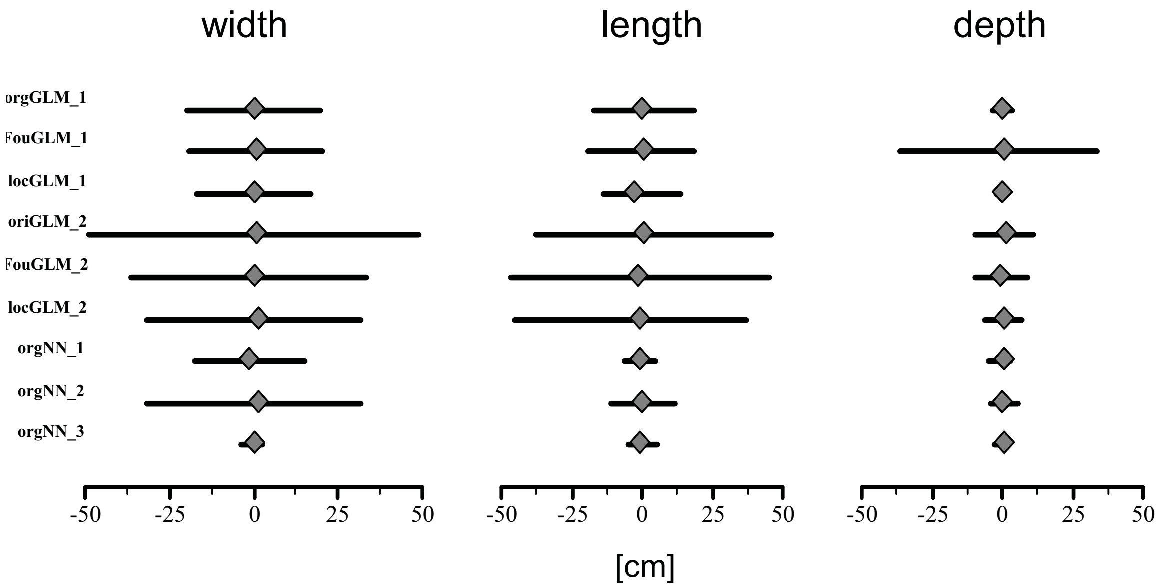

Figure 6.8: Errors of predictions with different antenna arrays and mathematical methods: Org= original not smoothed data, Fou= Fourier transformation smoothed data, loc= data smoothed by local regression; GLM= logistic regression used for prediction, NN= neuronal network used for prediction; _1=antenna array 1, _2= array 2; _3= array 3 (see text). Bars depict the 25 % quantile left of the median (diamond symbol) and the 75% quantile right of the median of the distribution of residuals in cm.

The predictions by logistic regression in general yielded smaller errors in antenna array 1 than in array 2 and larger errors after smoothing. Fourier transformation smoothing caused larger errors than local regression smoothing. Because calibration curves did not show a perceivable interference (small spikes of extremely high data in single points) and smoothing made predictions worse I applied the neuronal network algorithm only to the non smoothed calibration data.

The predictions of the neuronal network were better in all cases than the predictions of the logistic regression. With antenna array 1 the predictions were more accurate than with array 2. The largest problem in array 1 was the prediction of the width, since there were only two width antennae in each layer. I compared the values of these 4 width antennae with their equivalents in array 2 and found that the received signal strengths were quite similar (data not shown). Since these width antennae do not seem to be strongly influences by the addition of a third width antenna in each layer nor by the different spatial set up of the length antennae it seemed save to assume that the addition of another width antenna in each layer of array 1 would have yielded similar values. Thus I included the data of the additional width antennae to the calibration set of array 1 (this combination I call array 3) and applied the neuronal network algorithm again. The quality of predictions, depicted in Figure 6.8 as “orgNN_3”, was the best obtained from all calculations. The 25% quantile for array 3 was -4.96 cm and the 75 % quantile 5.68 cm in length, -3.95 and 2.75 in width, and –3.07 and 1.69 cm in depth, respectively. The maximum residuals were 9.8 cm in length, 6.2 cm in width, and 3.2 cm in depth. Therefore the inaccuracies are at most in the range of a few centimetres.

It is hard to depict the consequences these erroneous predictions might have on the swim paths of fish. Therefore I moved a transmitter through the tank simulating a fish swimming in a straight line over the entire length of the tank at a width of 50 cm and 20 cm below the water surface (Figure 6.9) in both antenna arrays and again constructed data for array 3 as described above. I thus obtained data that were not part of the calibration matrices. I predicted the locations using logistic regression for array 1 and 2 (Figure 6.9 A1+A2) and using the neuronal network algorithm for all 3 arrays (Figure 6.9 B1-B3) and plotted these against the actual locations of the transmitter (Figure 6.9). This confirms that array 3 (Figure 6.9 B3) yields the best results.

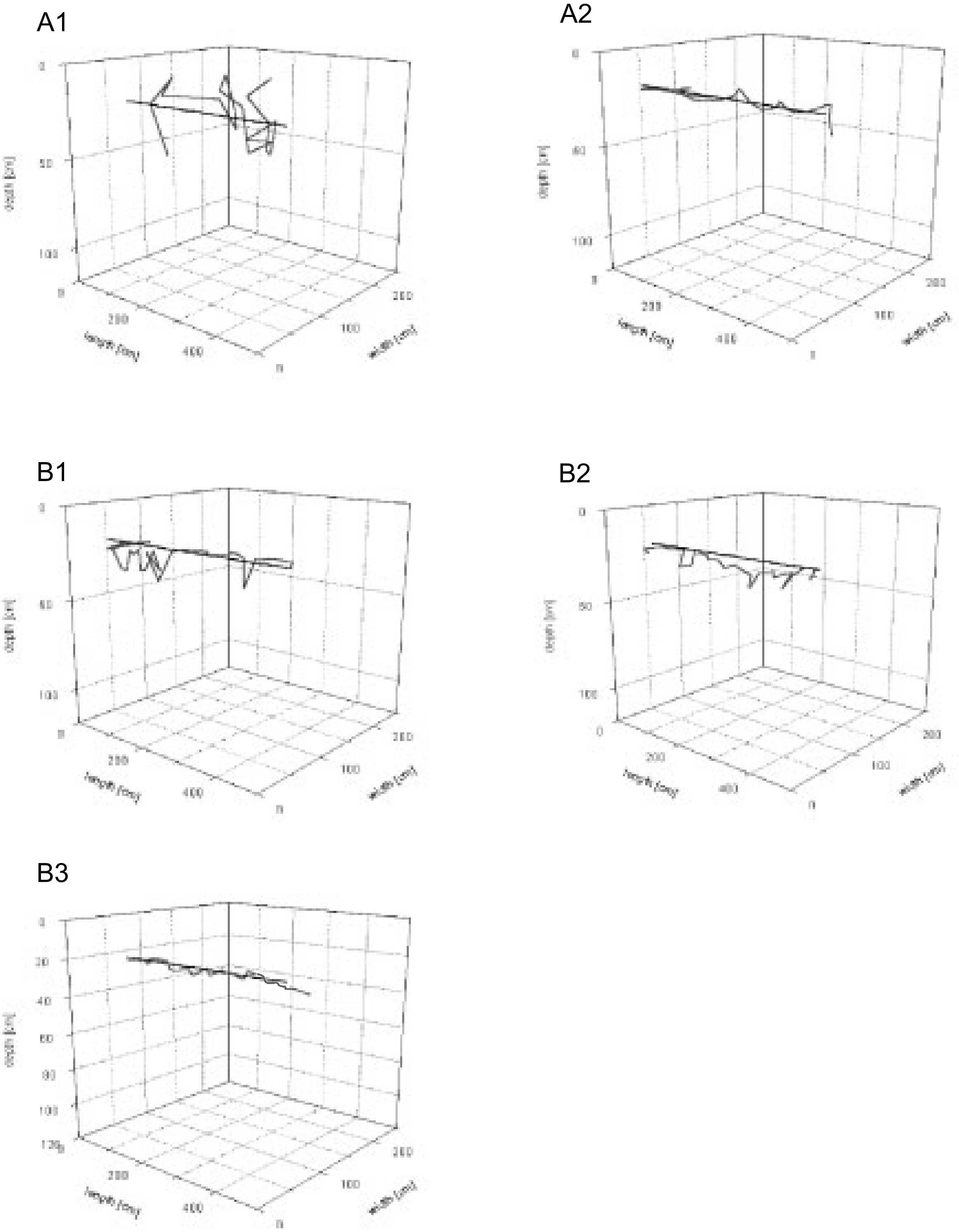

Figure 6.9: Measured (black) and predicted (red) positions plotted in 3D. **A**= Predictions on non smoothed data by logistic regression, **B**= Predictions on non smoothed data by neuronal network algorithm. Used were non smoothed data of **1**= array 1, **2**= array 2, **3**=the simulated array 3

6.5 Discussion

The developed telemetry system is suitable to address a detailed analysis of swim paths and thus far range as well as close range strategies of predators and prey in a nature-like structured tank. The transmitters developed are well within the range fish of the required size can carry and implantation into the abdominal cavity of prey or swallowing by the predator did not have a visible negative effect on the behaviour of the fish. The transmitters have the additional advantage that they are cheap to produce. The spatial precision of three-dimensional localisation of our developed method (a few cm at most) and the temporal resolution (two seconds) enable detailed studies on predator-prey interactions in a reasonably large environment. Adding more hidden nodes to the neuronal network algorithm and performing more learn steps will potentially further improve the spatial precision of the predictions. The largest errors were found at the surface close to the upper antenna array. Thus lowering the water level some 10 cm should further improve results. Even if the addition of one width antenna per layer as simulated in array 3 does not yield the predicted results the system in precise enough to be of great use.

To my knowledge this new system is the only telemetry method that is able to obtain such a high precision in three dimensions and the only automated system locating multiple fish with a temporal resolution of 2 seconds. Since data recording is automated it permits the gathering of a huge data set with minimal effort. The neuronal network algorithm that was best suited to predict locations has the advantage that once the network is trained (i.e. has performed many learn steps) the prediction of positions is very fast.

Most telemetry systems were developed to study homing or spawning migrations of fish, activity patterns, and home ranges on fairly large scales (meters to 100s of kilometres). There are only a few automated telemetry systems. Among them is satellite based telemetry applied to fish and marine mammals ranging freely in the ocean that requires large transmitters and operates over ranges of several hundreds of kilometres with spatial accuracy that is accordingly (at best some hundreds of meters) (see Baras, 1991 and references herein). Other automated systems are only capable of calculating 2 dimensional data (e. g. Stasko and Pincock, 1977). Hydrophone triangulation arrays depend upon a transmitter that is encoding depth (pressure) information in its signals to achieve the third dimension (e. g. Clark and Green, 1989; Hawkins et al., 1980). These transmitters are prohibitively large and heavy for our purposes. A couple of automated systems were developed to monitor fish migration in rivers. They consist of straight or looped antennae deployed every couple of meters or kilometres to detect fish that pass by (e. g. Breukelaar et al., 1998). Depth may be encoded in the signal pattern of the transducer but the third dimension, the width of the river, is missing here.

In addition to these automated systems there are a couple of methods where hand-held or boat-mounted directional receivers (directional hydrophones or antennae sets) are used to locate fish (e. g. Perrow et al., 1996; Savitz et al., 1983). The accuracy of these methods is mostly dependent on the operator and the distance between transmitter and receiver and is often not determined. I do not know of any automated method for multiple fish and with a temporal resolution as high as ours. For studying predator-prey interactions all these methods are not suitable due to their missing third (or even second) dimension, their large transmitters, their low temporal resolution, their inaccuracy in small scale dimensions or their time consuming manual sampling procedure.

Our observation of predator-prey interactions made by video under infrared illumination have a temporal resolution of 1/25 s. Judging from these findings in a spatially limited test tank one would miss a number of observed wave tracking events when sampling every 2 s. Our system was developed to track 10 different fish simultaneously. Reducing this number by half would double the temporal resolution of the system. The present rapid development in computer processor speed and other electronic devices may soon enable a still better temporal resolution. But the developed method already now provides a unique opportunity to study interaction of fish under a variety of conditions in much detail.

7 Conclusions and suggestions for future research

In the discussions of the previous chapters I have considered my presented new findings on predator-prey interactions of fish in the dark in respect to other studies. In the following section I will add some more speculative contemplation and suggest gainful future studies.

In the studies accumulated in this thesis I have investigated the interactions of predators and prey when they are already in each other's vicinity. This is only one, the final, part of predator-prey interaction. However, it is the part in which accuracy is most important and that will have the most dramatic results. In this last part of the interaction failure or success of both sides will be decided which is ultimately a matter of live and death. Thus I expect that this phase of the interaction should exert the strongest selective pressure on the sensory systems of fish. Preceding this final part of the interaction will include finding larger ranged profitable habitats, i.e. areas with high prey densities for predators and areas with refuges and low predation pressure for prey, and foraging strategies that increase the probability to encounter directional cues.

I found a hitherto unknown strategy that nocturnal piscivors employ to locate their prey, namely tracking the hydrodynamic wake of swimming fish. My novel mathematical approach permits the quantitative comparison of swim paths.

In contrast to other directional information emanating directly from a prey wakes represent the past locations of the prey. Tracking wakes leads the predator to approach the prey fish from behind. This is an advantage for the predator and a disadvantage for the prey, since most sensory systems are best developed to detect stimuli in the head region of a fish: The eyes are located to look frontally and sideways, the lateral line is most refined in the head region of a fish, the nose is located frontally at the head, respiratory movements are drawing in water from in front that is subsequently passed along the taste buds inside the mouth cavity and the gills, and external taste receptors have their highest densities on the head of a fish. Thus potential prey will be least aware of a predator approaching from behind, while a predator can receive all information before it is disturbed by its own body motions.

The finding that the lateral line is employed in this behaviour shows an important behavioural aspect of the function of lateral lines. Like the finding that surface feeding fish utilise surface waves of struggling insect prey (Bleckmann, 1980, 1985, 1988) wake tracking should spur physiological studies with this natural stimulus as well as physical measurements of the hydrodynamic characteristics of wakes under ambient flow conditions found in lakes. Wake tracking can potentially be applied by a large variety of predators and due to the differences in fluid dynamics operating at different scales might require different properties of mechanosensory systems.

Bell lists five general principles concerning the use of directional orientational information (Bell, 1991) that are applicable to the wake tracking behaviour I observed and other orientation strategies reported elsewhere for catfish:

1. Perception of directional information may cause an animal to switch over from its initial searching mode based on non-directional sensory or internally derived information to directional information to control its orientation.

We observed catfish swimming around searching until they encounter a hydrodynamic trail and then switching to the use of the directional hydrodynamic information. The same is expected before catfish encounter a chemical gradient (as reported for stationary food) or an electric field giving them directional information .

2. The type of information an animal uses may be dependent upon the context or the immediate environmental conditions.

Catfish could potentially use hydrodynamic information of wakes of resting prey in ambient flow as they were using wakes of swimming prey in the absence of directional ambient flow to determine the position of live fish. They were further shown to utilise chemical gradients to locate stationary food items in stagnant water. If there is, however, any ambient turbulent flow there is no reliable chemical gradient. Recent studies indicate that in chemical odour plumes in turbulent flows neither time averaged concentrations, nor rise slopes, nor burst shape measured at a single or many closely spaced receptors would be sufficient to locate an odour source (Webster and Weissburg, 2001). However, if an animal’s sensors are spaced wide enough apart they can detect the centreline of the plume and the distance of the source through bilateral comparison of chemical concentrations (Webster et al., 2001). Catfish can make use of this strategy since their long barbels, which are densely covered with taste buds (Atema, 1971), are held wide apart during searching. They were shown to turn to the side of higher chemical concentration when their barbels were stimulated differently (Johnsen and Teeter, 1980). Physical measurement in natural habitats of catfish are needed to determine the potential use of the stimuli under different conditions.

3. Up to a point, the accuracy of orientation improves with stimulus intensity.

This is certainly true for wakes that deteriorate and spread over time. The closer a catfish is to the source of a wake the stronger the hydrodynamic signal and the easier it becomes to follow a trail.

4. The precision of directional orientation varies according to the modality, so that animals may switch from less precise to more precise modalities when given the opportunity.

I think that the interpretation of different orientation modalities described above may be a good example for this. If wakes are present the catfish utilises these and does not require chemical information to locate its prey. If a stationary food item is oozing chemicals gradient search is employed in the absence of directional currents. If there is no large electric noise in the surrounding they may use their electroreception to locate live prey.

5. Most animals integrate directional cues from more than one modality.

We found that catfish do not need the chemical information in the wake to track it. Chemical information alone proved to be insufficient to track wakes. This does not rule out the possibility that unimpaired catfish use both chemical and hydrodynamic stimuli in the wakes or that close to the prey other sensory inputs supplement the wake tracking.

To address the question how often wake tracking is employed under natural conditions and which conditions allow or restrict its utilisation behavioural experiments along with physical investigations are needed in a larger and naturally structured environment. The lack of suitable methods has precluded this kind of investigation so far. By developing a mathematical method to compare swim paths of predator and prey quantitatively (see chapter 2) and by developing a technique that is able to automatically track swim paths of multiple fish in a reasonable temporal and spatial resolution over extended time intervals (see chapter 6) I provide the basis for this future research.

Comparative studies revealed that another nocturnal piscivor, the burbot *Lota lota*, does not utilise wakes from swimming prey fish but seems to require minute amounts of visible light to locate piscine prey. The distribution and swimming behaviour of different prey species in the dark as well as their sensory sensitivity seems to have an effect on the encounter probability with burbot. By comparing the behaviour of catfish and burbot under similar experimental conditions I could obtain evidence that not all nocturnal piscivors make use of the wakes of their prey. By skilfully designing experiments one can find out that animals are able to perform certain tasks. If they do *not* show the hypothesised behaviour, however, they still may be able to but under the given circumstances decide to not perform. Because of the context-dependent plasticity of animal behaviour a negative result may just mean that under the given conditions the animal does not make use of the strategy in question. Comparing different species under identical experimental conditions strengthens the evidence that the failure to perform a certain behaviour by one but not the other species in fact represents an inability to institute this strategy. It is no ultimate proof, however, although morphological comparisons and incidental behavioural observations reported in chapter 4 point in the same direction. The next step should be to compare predation success of burbot and catfish under different experimental conditions, e.g. minute intensities of visible light.

Nocturnal predators occupy a niche where there is no competition from diurnal predators and where prey organisms are less evasive. If, in addition, they employ different sensory modalities for locating prey this might lead to a microhabitat segregation that further limits competition. If future experiments verify the evidence obtained in this study that burbot use minute amounts of light to visually locate prey fish catfish could avoid competition by feeding in areas were no vision at all is possible. This might be a reason why catfish are often found in eutrophic lakes while burbot are mostly present in oligotrophic or mesotrophic waters where the water’s transparency allows vision even at night.

I have shown that, contrary to earlier findings, released conspecific alarm substance (which indicates an elevated risk of predation) elicits a reaction of potential prey fish in the dark. Juvenile dace reduce locomotion and vertical area use. The knowledge of different predatory strategies enabled me to deduce that the observed behavioural changes are apt to reduce predation. The cessation of locomotion limits the detectability of the prey to wake tracking predators. Given that most nocturnal predators are slow moving and that prey are swimming in the same range of velocities locomotion would increase the encounter probability with predators even if they did not utilise the wake.

I have discovered that differences in horizontal distribution between different prey fish led to different encounter rates with burbot even in our small test tank.

However, our experimental design precluded some potential avoidance reactions. From the second minute after alarm substance addition onwards there were similar concentrations throughout the whole tank and thus no areas of high concentrations that fish could avoid. Area avoidance in natural environments could lead to shifts into low risk habitats equivalent to vertical migration of zooplankton. Occupying structures that are inaccessible to larger predators upon the perception of danger would be another option for prey to reduce predation pressure. To study these kinds of behaviour a larger and structured tank or, ideally, investigations in the field are required. Again, the developed telemetry method will enable first steps to study these questions.

It should also be rewarding to study direct effects of the observed antipredator response on the survival of juvenile fish in the dark as has been done in light (Mathis and Smith, 1993). Olfactory impairment, which is simply achieved by plugging the nares, disables chemical predator recognition through alarm substances and learned cues (Chivers and Smith, 1993). Thus an experiment comparing the capture success of a predator on olfactorily impaired and intact prey in the presence of alarm substance can answer this question.

Besides avoiding areas of high predation and shifting to habitats that are less or not accessible to predators prey can also try to reduce detectability. There are very few mechanisms reported through which fish can camouflage from other than visual detection. Reducing motion is certainly appropriate to reduce hydrodynamic cues and avoid spreading chemical information any more than ambient flow does. A fascinating mechanism to prevent the spreading chemical of fish are the “mucous pyjamas” of parrotfish (Shephard, 1994; Winn, 1955; Winn and Bardach, 1956). These tropical fish rest at the bottom under coral reef structures at night and envelope themselves in a cocoon of mucus that, among other properties, prevents exudates from spreading. The antipredator value has been demonstrated (Shephard, 1994; Winn and Bardach, 1956). This has never been reported for other fish. However, resting or at least reducing locomotion permits to reduce metabolism and thus may reduce exudation, too. Slow respiration and reduced exudation also deminish the strength of the electrical field around a fish, both the AC and DC component (Peters and Bretschneider, 1972).

Our findings that dace exposed to alarm substance are descending to the bottom as well as the fact that many fish species are resting on the ground at night seems counterintuitive at first because most nocturnal predators are swimming along the bottom. I assumed that this behaviour is just a consequence of the cessation of swimming, but there still may be other reasons. If an animal loses all fixed points of reference and there is ambient flow, it loses control over where it is. Assuming that illumination at night is too weak for fish without special adaptations to visually determine their absolute location they may have to stay in touch with the bottom substrate to hold their position. Remaining in an area or at least knowing where to return to is important for fish that aim to stay in a profitable area with refuges and food for day time. If ambient currents in different heights above ground differ in velocity or even direction, drift of fish may also scatter groups that in day time form a school.

In order to understand the spatial distributions of organisms it is essential to understand which processes influence them. The absence of populations or subpopulations from a certain habitat can be as informative as, or even more than, an organism's presence (Begon et al., 1996). Abiotic factors such as temperature and oxygen set limits on where individual fish can survive. They are, however, not influenced by an organism's response. In contrast predator-prey interactions have consequences for the involved organisms. They influence the distribution, abundance, and genetic composition of the populations of which the interacting organisms are members as well as for the species composition of the assemblage at a given location (Wootton, 1998). These consequences result from the effects of the interactions on the individual participants. One cannot understand these consequences without analysis of individual predator-prey interactions including both sides of the interaction. Thus the evidence obtained in this study contributes essential mosaic pieces in the hitherto hardly studied area of nocturnal predator-prey interactions of fish that has major influence on the structure of communities as well as the evolutionary development of sensory capabilities.

8. Summary

This thesis summarises a series of laboratory experiments on the central issue of strategies employed in nocturnal predator-prey interactions of fish. I investigated the interaction of piscivorous European catfish (*Silurus glanis*) and burbot (*Lota lota*) with several species of prey fish in the absence of visible light as well as the prey's reaction to perceived risk of predation.

European catfish (*Silurus glanis*) were found to employ a hitherto unknown predation strategy to locate swimming piscine prey (guppy *Poecilia reticulata;* dace *Leuciscus leuciscus*): they were accurately tracking their prey's three-dimensional swim path prior to an attack. Wakes that were up to 10 s old were followed over distances up to 55 prey body lengths in my experimental set-up. In a wake there is hydrodynamic as well as chemical directional information. A functional lateral line proved indispensable to follow wakes of swimming prey while catfish with ablated external taste still followed the wakes of their prey prior to attacks.

Comparing the predatory behaviour of catfish to that of burbot under identical experimental conditions revealed two different strategies. Burbot did not utilise wakes and their capture rates were much smaller than those of catfish and similarly low on all offered prey species (juvenile perch *Perca fluviatilis*; ruffe *Gymnocephalus cernuus*; dace *Leuciscus leuciscus;* bream *Abramis brama*). Morphological comparisons and behavioural observations lead to the conclusion that burbots are primarily visual predators of live piscine prey even at night. The different encounter frequencies of burbot could be explained by different spatial preferences and sensory sensitivity of the prey species.

Another set of experiments was designed to focus entirely on the prey's side of the interaction. Released alarm substance enables potential prey fish to chemically assess predation risk and elicits an innate fright response in conspecifics that serves to reduce the susceptibility to predation in light, while such reaction was claimed to be absent in the dark. I found that dace (*Leuciscus leuciscus*) significantly decreased their activity and reduced vertical area use when exposed to conspecific alarm substance in the dark. This behaviour is effective in reducing the susceptibility to wake tracking predators as well as nocturnal visual predators perceiving their prey's silhouette against a faintly lit background.

A lack of appropriate methods has prevented the study of interactions of fish in the dark in larger and naturally structured environments. Therefore, I developed a radiotelemetry system that determines the position of up to 10 fish in three dimensions with a temporal resolution of 2 seconds over several hours or even days. This system is a unique tool for future larger scaled studies of nocturnal interactions of aquatic organisms.

Zusammenfassung

Diese Dissertation faßt eine Reihe von Laborexperimenten zusammen, die sich mit den Strategien von Fischen in nächtlichen Räuber-Beute-Interaktionen beschäftigen. Hierbei habe ich die Interaktionen von piscivoren Welsen (*Silurus glanis*) und Trüschen (*Lota lota*) mit zahlreichen Beutefischarten bei Infrarotbeleuchtung untersucht, sowie die nächtlichen Reaktionen potentieller Beutefische auf Exposition von arteigenem Schreckstoff, der die Nähe eines aktiven Prädators signalisiert.

Welse verfolgten exakt die Pfade schwimmender Beutfische (Guppies *Poecilia reticulata;* Haseln *Leuciscus leuciscus*), um diese zu orten. Dies ist eine bislang unbekannte Prädationsstrategie. Pfade, die bis zu 10 Sekunden alt waren, wurden hierbei über Strecken von bis zu 55 Beutefischlängen verfolgt. Der Nachlauf von Fischen enthält sowohl chemische als auch hydrodynamische Richtungsinformationen. Anhand von Ausschaltexperimenten konnte ich zeigten, daß für die nächtliche Verfolgung von Schwimmpfaden eine intakte Seitenlinie unabdingbar ist, die Welse also den hydrodynamischen Richtungsinformationen der Wirbelstaßen folgen, während sie mit ausgeschaltetem externen Geschmackssinn noch in der Lage waren, die Schwimmpfade zu verfolgen.

Im Vergleich zu Welsen erzielten Trüschen unter identischen experimentellen Bedingungen wesentlich geringere Fangerfolge und nutzten die Wirbelstraßen der Beutefische (juvenile Flußbarsche *Perca fluviatilis;* Kaulbarsche *Gymnocephalus cernuus*; Haseln *Leuciscus leuciscus;* Brachsen *Abramis brama*) nicht. Morphologische Betrachtungen und einige Verhaltensbeobachtungen legen den Schluß nahe, daß Trüschen Sehspezialisten sind, denen schon geringste Restlichtmengen ausreichen, um ihre Beute optisch zu lokalisieren. Trüschen trafen häufiger auf Beutefische, die am Boden ruhten, als auf jene, die sich in der Wassersäule aufhielten, was zeigt, daß die räumliche Verteilung einen Einfluß auf das Prädationsrisko haben kann.

Des weiteren untersuchte ich Vermeidungsstrategien potentieller Beutefische, die chemisch ein erhöhtes Prädationsrisiko wahrnehmen. Juvenile Haseln wurden arteigenem Schreckstoff ausgesetzt, der eine hohe Prädationsgefahr signalisiert und angeborene Verhaltensänderungen im Hellen auslöst, die das Prädationsrisiko

herabsetzten. Obwohl bislang berichtet wurde, daß Schreckreaktionen im Dunkeln ausbleiben, zeigten die Haseln eine signifikante Reduktion ihrer Schwimmaktivität sowie eine deutlich reduzierte vertikale Raumnutzung. Dieses Verhalten vermindert einerseits das Risiko von Prädatoren gefressen zu werden, die die Wirbelstraßen verfolgen, andererseits auch das durch nächtliche visuelle Prädatoren, die die Silhouette ihrer Beute gegen einen schwach beleuchteten Hintergrund wahrnehmen.

Fischverhalten im Dunkeln wurde aufgrund fehlender Methoden in größeren und natürlich strukturieren Systemen bislang nicht untersucht. Deshalb entwickelte ich ein radiotelemetrisches System, das gleichzeitig dreidimensionale Aufenthaltsorte von bis zu 10 Fischen in zeitlichen Intervallen von 2 Sekunden über mehrere Stunden oder Tage hinweg ermittelt. Diese Methode ist aufgrund ihrer hohen räumlichen und zeitlichen Auflösung hervorragend geeignet, um grundlegende Untersuchungen über großräumigere Interaktionen nachtaktiver aquatischer Organismen durchzuführen.

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