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 1µV 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).