UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING AND THE ENVIRONMENT

Centre for Environmental Sciences

Civil, Maritime, and Environmental Engineering and Science

Quantification of the collective response of fish to hydrodynamics for improving downstream fish passage facilities

by

Jasper de Bie

Thesis for the degree of Doctor of Philosophy

April 2017

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

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Migrating freshwater fish species are limited in their longitudinal movements due to barriers representing anthropogenic water resource management. Technologies, such as physical screens, designed to mitigate the effects of these obstacles on downstream migrating fish, are currently not functioning to a high standard, due to a lack of understanding of the response of fish to hydrodynamics encountered at screens. Furthermore, collective behaviour is often not considered in this context. This thesis addresses these issues through experimental studies conducted in recirculating flumes.

There is a lack of understanding on the fundamental interactions that underlie collective fish movement in lotic conditions. To address this, the shoal structure and interaction rules of pairs of Eurasian minnow, *Phoxinus phoxinus*, were studied under flowing conditions and standing water, and energy expenditure in terms of drag modelled using CFD software. Results indicate that flow promotes shoaling but induces a change in shoal structure due to individuals aiming to maximize information transfer rather than exploiting energetic benefits.

Besides economic important species, such as salmonids, the wider fish community is often ignored in fish screening research. Several experiments were carried out to assess the performance of bar racks and wedge-wire screens for downstream moving small groups of chub, *Squalius cephalus*, and barbel, *Barbus barbus*, under two discharge regimes. A horizontal alignment of bars was, for the first time, compared to the traditionally used vertical alignment in terms of hydrodynamics created at the screen and performance.

Horizontal and vertical bar racks did not differ in the flow fields they induced, with mean flow primarily directed going through the racks. Avoidance responses were stronger in chub than barbel, but for both species this resulted in high numbers of entrained fish, regardless of rack configuration or discharge regime. Wedge-wire screens with a small bar spacing to eliminate entrainment seemed efficient in guiding chub, although strong avoidance behaviour was observed. Vertical wedge-wire screens induced higher sweeping velocities along the screen, however the horizontal one under low discharge produced highest guidance efficiency. The experiments confirm the importance of avoidance behaviour to hydrodynamics in the context of successfully fish screening. Shoal cohesion was weak for both species, and warrants further research into identifying the factors responsible.

The results presented in this body of research are an important step to a better understanding of how fish respond to flow, which can have implications for collective modelling of animal movements in complex environments. Furthermore, it helped improve screen design criteria for the fish species used. In turn, this will help maintaining healthy fish populations that can benefit freshwater ecosystems.

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DECLARATION OF AUTHORSHIP

I, Jasper de Bie,

declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

QUANTIFICATION OF THE COLLECTIVE RESPONSE OF FISH TO HYDRODYNAMICS FOR IMPROVING DOWNSTREAM FISH PASSAGE FACILITIES

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. None of this work has been published before submission.

Signed: ....

Date: ....

Acknowledgements

This thesis would not have been made possible without the support of many people along the way. Firstly, my sincerest thanks to my first supervisor, Prof. Paul Kemp, and second supervisor, Assoc. Prof. Costantino Manes, for their continuous enthusiasm and guidance during my PhD. I remember the day I first arrived on Highfield Campus after a 9 hour drive from the Netherlands, 5 minutes before my application interview was due to start, and the fruitful conversation we had about this project. I am very happy I decided to take it on and thankful to have completed it with your assistance.

Though I only met one other colleague from our ‘Team Fish’ that day (‘I don’t know where they are but they should be working here’ – Paul), I would not have completed this work without the office/ pub conversations and discussions about experimental setups and data analyses with my colleagues. Not to mention their assistance during my experimental trials in Chilworth. Thank you so much Jim, Andy, Gill, Lyn, Laura, Adam, Maty, Matt, Rob, Daniella, Helen and Nick. Particular thanks go out to Jim and Andy who made me feel welcome in Southampton from the day I started working here. I would like to thank Graeme Peirson and Greg Armstrong (EA) for their technical advice on the setup of the screen experiments; and to Alan Henshaw and his team for supplying me with the fish.

I would further like to thank my friends in the UK and back home, who are not so familiar with the world of Ecohydraulics and to whom I had to explain on many occasions what I was doing and more importantly, why. Thanks for visiting me, hosting me and allowing me to escape University and work for those moments to talk about something else besides science!

To my parents, my sister Marije, and other family members, thank you so much for your continued support and motivational words when I needed them. I always wanted to pursue a PhD and without you, I would not have been able to start, let alone finish one.

Finally, to Karlien, words cannot express how thankful I am for your support over the last few years, especially during the final write-up. I will do my best to be there for you too when you enter the final stages of your PhD.

This research was funded by the EPSRC on DTA Grant 11, with additional funding from the Environment Agency.

Glossary of Terms

A: Fish families

COMMON NAME	LATIN NAME
Cichlids	Cichlidae
Cod	Gadidae
Eel	Anguillidae
Herring	Clupeidae
Lamprey	Petromyzontidae
Mackerels	Scombridae
Minnows or carps	Cyprinidae
Mullets	Mugilidae
Salmon	Salmonidae
Smelt	Osmeridae
Sticklebacks	Gasterosteidae
Striped basses	Moronidae
Sturgeon	Acipenseridae
Sunfish	Centrarchidae
Toothcarps	Poeciliidae

B: Fish species

COMMON NAME	LATIN NAME
American eel	*Anguilla rostrata*
American shad	*Alosa sapidissima*
Atlantic bluefin tuna	*Thynnus thynnus*
Atlantic salmon	*Salmo salar*
Barbel	*Barbus barbus*
Blue acara	*Aequidens pulcher*
Blackfin shiner	*Notropis heterodon*
Brown trout	*Salmo trutta*
Cape Fear shiner	*Notropis mekistocholas*
Creek chub	*Semotilus atromaculatus*
Chub	*Squalius cephalus*
Cod	*Gadus morhua*
Delta smelt	*Hypomesus transpacificus*
Eurasian minnow	*Phoxinus phoxinus*
European eel	*Anguilla anguilla*
Giant danio	*Devario aeguipinatus*
Golden shiner	*Notemigonus crysoleucas*
Goldfish	*Philoponella republican*
Grey mullet	*Liza aurata*
Guppy	*Poecilia reticulata*
Herring	*Clupea harengus*
Lake sturgeon	*Acipenser fulvescens*
Mosquitofish	*Gambusia holbrooki*

Palmetto bass	*Morone chrysops* x *M. saxatilis*
Rainbow trout	*Oncorhynchus mykiss*
River chub	*Nocomis micropogon*
River lamprey	*Lampetra fluviatilis*
Roach	*Rutilus rutilus*
Saithe	*Pollachius virens*
Sea bass	*Dicentrarchus labrax*
Shortnose sturgeon	*Acipenser brevirostrum*
Silver shiner	*Notropis photogenis*
Smallmouth bass	*Micropterus dolomieu*
Sockeye salmon	*Oncorhynchus nerka*
Splittail	*Pogonichthys macrolepitodus*
Three-spined stickleback	*Gasteroseus aculeatus*

C: General terms

Abiotic: Non-living physical or chemical attribute of a system.

Acceleration: Increasing rate of velocity change over time.

Acclimation: To accustom or become accustomed to a new environment.

Anthropogenic: Of, relating to, or resulting from the influence of human beings.

Bar rack/ trash rack: Type of physical screen used to block fish entry to water intakes and divert them to a safe bypass. Usually consists of vertical oriented bars slotted into a frame.

Behavioural screen: Facility which exploits the fish's sensory system to deter them from a certain location (usually an intake).

Benthic: Relating to, or living near the bottom of a body of water.

Bypass: A safe route for downstream moving fish past riverine barriers.

Channel velocity: Main velocity component in front of a fish screen, in the direction of the mean flow.

Coarse fish: Freshwater fish that is not a member of the Salmonidae.

Deceleration: Decreasing rate of velocity change over time.

Diadromous: Migratory between salt and fresh water environments. Depending on life history, fish species are sub classified as anadromous (spawning in fresh water) or catadromous (spawning in salt water).

Drag: A mechanical force, generated by the interaction of solid bodies with a surrounding fluid, that acts in the opposite of the direction of movement.

Entrainment: 1) Pulling, or drawing along after itself. This is a certain type of behaviour is found in fish near obstacles, for the purpose of maintaining position and reducing energetic expenditure (Liao, 2007). 2) unwanted passage of fish through a water intake, usually the consequence of inadequate screen functioning.

Escape velocity: Component of the channel velocity perpendicular to a fish screen. Relative to the swimming capabilities of fish, this component should be low enough to prevent entrainment/ impingement (O'Keeffe and Turnpenny, 2005).

Fish pass/ fishway: A structure on or around anthropogenic barriers that dissipates the energy of falling water over a series of steps (e.g. pools) to enable upstream fish passage. ‘Fishway’ is the more commonly used term in North America.

Guidance efficiency: The number of fish guided into a bypass as proportion of the combined numbers of guided and entrained fish.

Habitat: The natural environment of an organism.

Habitat connectivity: The manner in which organisms are capable of moving between different habitats.

Hydraulic: Referring to liquids in motion, synonymous to ‘hydrodynamic ‘.

Hydrodynamic: Pertaining to forces in or motions of liquids.

Impingement: Prolonged physical contact of a fish with a structure, usually as a consequence of a high flow velocity.

Interspecific: In reference to something between species.

Intraspecific: In reference to something within species.

Lateral line: Mechanosensory organ, unique to fish and amphibians, that serves to detect movement and pressure changes in surrounding water.

Lentic: Pertaining or living in standing water.

Lotic: Pertaining or living in flowing water.

Louver screen: Semi-behavioural type of fish screen, i.e. it is a physical screen but it exploits the fish’s avoidance of turbulence to guide them to a bypass.

Migration: The round-trip, seasonal movement of organisms among two (or more) locations (Shaw, 2016).

Ontogenetic: Of, relating, or appearing in the course of the development of an organism.

Physical screen: A device placed in the waterway to physically exclude fish from entering hazardous areas, and guide them to a safe alternative route (see ‘bypass’).

Potamodromous: Migratory within fresh water environments.

Rheotaxis: A form of movement in response to the direction of water flow. Positive rheotaxis is the turning of fish to face the oncoming flow. Negative rheotaxis is the turning of fish with the flow.

School: A set of individuals adopting shoaling behaviours, living in a group and adopting a significant degree of synchronisation of displacements (in speed and polarity terms) resulting from social interaction between these individuals.

Self-organization: A process in which a pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of the system (Camazine et al., 2003).

Shoal: A set of individuals presenting a significant degree of cohesion, limited in a relatively small portion of space, a consequence of a social interaction between these individuals.

Smolt: A young salmon or sea trout that is at the stage of development when it assumes the silvery colour of the adult and is ready to migrate to the sea.

Sweeping velocity: Component of the channel velocity parallel to a fish screen. A suitable sweeping velocity should improve fish guidance to a bypass channel (O'Keeffe and Turnpenny, 2005).

Thigmotactic: Moving in close proximity to solid bodies (e.g. the channel floor and walls).

Turbulence: Chaotic vertical flows of multiple strengths and sizes superimposed on the mean flow velocity (Liao, 2007).

Velocity gradient: The change in velocity over a given distance.

Wedge-wire: Type of material used in fish screens. It consists of V shaped surface profile wires that are welded onto support profiles.

Chapter 1: Thesis Introduction

1.1 Introduction

One of the major evolutionary transitions that describe the patterns of biological complexity is the formation of social groups from solitary individuals (Szathmary and Smith, 1995, Bourke, 2011). Living in groups is ubiquitous throughout the animal kingdom, from tiny microbes (West et al., 2007) to large species of cetacean (Gero et al., 2014). Therefore, being gregarious is presumably beneficial over living a solitary existence. This is explained by fitness enhancing factors, such as anti-predatory defence and foraging strategies, although certain costs, such as increased parasitic burden, can also be incurred (Krause and Ruxton, 2002). For the formation, maintenance, and functioning of groups, social transmission of information is crucial. This emergence of group patterns following member-interactions is termed self-organization and results in the collective behaviours displayed by groups during movements or when responding to outside perturbations (Camazine et al., 2003, Couzin and Krause, 2003).

An essential part of the lifecycle of many animal species, linked to group formation, is migration (Dingle, 1996). It is defined as the persistent and straightened out movements and relocation of animals on greater spatial and temporal scales than during normal daily activities (Dingle and Drake, 2007). The main motivations for migration is a response to environmental conditions, but often linked to feeding and reproduction purposes (Shaw, 2016). For instance, ungulates aggregate annually before following seasonal vegetation growth (Berger, 2004, Harris et al., 2009); birds migrate between wintering and breeding grounds annually (Dingle, 2009); fish migrate within or between fresh and salt water for annual spawning (Lucas and Baras, 2001, Secor, 2015), and insects too have been found to cover substantial distances for reproducing (Chapman et al., 2015). Specific benefits of migrating together with conspecifics are thought to be energetic benefits when adopting a suitable group structure, such as a V-formation in birds (Fish, 1999), or enhanced navigational accuracy (‘many wrongs principle’) (Simons, 2004). As migrants move around, they perform essential ecosystem services (e.g. nutrient transport) and thus play a vital role in global biodiversity (Bauer and Hoye, 2014).

Animal migration across the world is strongly affected by anthropogenic interference (Wilcove and Wikelski, 2008). One such anthropogenic interference is the presence of physical barriers along animals’ migration routes both on land and in waterways (Wilcove and Wikelski, 2008). On land, fences are primarily used in Africa to protect humans, crops and cattle from wildlife (Boone and Hobbs, 2004), however, these fences also show a blocking effect on migrants in for example Blue wildebeest (*Connochaetus taurinus*) in South-Africa and Botswana (Whyte, 1988, Spinage, 1992). More recently, the implementation of numerous fences in Europe aimed to counter an influx of human refugees has been linked to negative impacts on migratory species such as the red deer (*Cervus elaphus*) (Linnell et al., 2016). In waterways, dams have been implemented for irrigation and water supply purposes for thousands of years, (Sternberg, 2006). According to the World Commission on Dams, more than 45,000 dams above 15m high existed in 2000 (WCD, 2000), and this has grown to over 58,000 at present (ICOLD). In addition to dams, thousands of smaller barriers (e.g. weirs) are present throughout Europe (Paish, 2002). The impact of them ranges from flow alteration and physical and/or chemical processes to changes in biodiversity (Petts, 1980, Fahrig, 2003, Liermann et al., 2012). Migrating fish can be impeded or blocked in both their upstream and downstream movements depending on the type of barrier, river characteristics and interspecific differences such as swimming capabilities

(Northcote, 1998). When moving downstream, migrants can furthermore be entrained at water intakes or suffer injuries through alternative pathways (Coutant and Whitney, 2000). These anthropogenic barriers have already contributed to freshwater fish species being the most threatened vertebrate species (Bruton, 1995), and loss of biodiversity is expected with increasing human population size and economic growth worldwide (Clausen and York, 2008). With this in mind, well-studied strategies for mitigation and conservation are required.

To mitigate the impacts of riverine barriers for migrating fish, different strategies have already been employed in the past (Clay, 1995, Katopodis and Williams, 2012). To promote upstream movements, fish passes divide the height difference between the upper and lower reaches of the barrier into a sloping channel that fish can negotiate; and screening systems attempt to minimize entrainment and/or impingement at intakes while guiding fish to safer alternative routes, such as a bypass channel (Taft, 2000, Katopodis and Williams, 2012). Increased acknowledgement of negative impacts of barriers has further led to acts of legislation throughout the world (Kemp, 2016), which generally require the presence of passage facilities or screening systems to protect migrants. An example of such legislation is the Water Framework Directive in Europe (WFD, 2000/60/EC) and the Federal Power Act in North America (Kemp, 2016).

Historically, research on the evaluation of fish passes is more advanced than that of screening systems (Katopodis and Williams, 2012). The efficiency of fish passes should generally be above 90% to ensure stable populations (Lucas and Baras, 2001), yet most fish passes do not perform to this standard (Bunt et al., 2012, Noonan et al., 2012). While a global assessment of fish screening efficiency has not been carried out, research indicates that screens do also not meet efficiencies over 90% (e.g. Gessel et al., 1991, Calles et al., 2013). For upstream migrants, both the behavioural response to hydrodynamics and their swimming capabilities determine whether they access and ascend fish passes, but for downstream migrants, their behavioural response is likely of higher significance (Castro-Santos et al., 2009, Williams et al., 2012). Many fish species form groups, especially as juveniles (Shaw, 1978) and, being weak swimmers, they are particularly susceptible to injury/ mortality if screens do not protect them from entering intakes. To protect fish in this vulnerable life stage, further research is warranted that, in a dual approach, assesses the performance of screens for a variety of species, and provides a better understanding of how fish groups collectively respond to flow.

1.2 Thesis aim and objectives

The general aim of this thesis is as follows:

I. To advance scientific knowledge to aid the downstream passage for gregarious fish species.

To meet this aim, an initial objective is formulated:

i. Review current literature to identify research trends, knowledge gaps and opportunities to improve downstream fish passage for gregarious fish species.

1.3 Thesis overview

A literature review as undertaken to meet Objective i, and is presented in Chapter 2. This will identify further research objectives to meet the general aim. To fulfil these objectives, several experiments were conducted, of which general methodologies are described in Chapter 3. In each of the results Chapters 4-6, the conducted experiments are introduced and reported as stand-alone bodies of research. Each chapter relates to specific research objectives, which are summarised and presented in a schematic overview at the end of Chapter 2. In the final Chapter 7, all the results are combined, evaluated, and discussed in relation to the thesis aim. An evaluation of how the results of this body of research can be incorporated into future fish screen design is presented here, as well as directions for future research in this context.

Chapter 2: Literature Review

Through billions of years of evolution, biological units have increased in complexity (Szathmary and Smith, 1995). This is assumed to have occurred via a series of major evolutionary transitions, that involve changes in the way information is stored and transmitted (Bourke, 2011). Examples of these transitions include the formation of eukaryotes from prokaryotes, that of multicellular organisms from protists, and that of colonies from solitary individuals (Szathmary and Smith, 1995). Group living is now an ubiquitous feature throughout the animal kingdom, e.g. found in microbes (West et al., 2007), insects (Meunier, 2015), fish (Shaw, 1978), and mammals (Gero et al., 2014). For individuals to join and stay in a group, it must offer certain benefits that would not be incurred when alone. It follows that group members help maintain the group and thereby serve their own interest (Alexander, 1974). However, as many species live a (partially) solitary life, grouping must bring costs along as well.

2.1 Benefits of group formation

There are several ways in which grouping offers protection from predatory threats (‘safety in numbers’). These include the dilution of risk, reduced need for vigilance, selfish herding, predator confusion or communal defence. Dilution of risk means that the danger of a predatory attack is divided among members of the group, and the larger the group is the smaller the chance of being targeted. However, predation and survival are strongly dependent on other factors as well, such as the detectability of the group, whether multiple targets are caught in a single attack and the success rate of predators, which complicated an accurate mathematical description of the dilution effect (Lehtonen and Jaatinen, 2016). Empirical evidence for the dilution effect has been found, e.g. for breeding groups of *Liostenogaster vechti* and *L. flavolineata* wasps in response to parasites (Coster-Longman et al., 2002) and ocean skaters, *Halobates robustus*, under attack from pilchards, *Sardinops sagax*, (Foster and Treherne, 1981).

In groups, there are many individuals who could possibly detect a predator (i.e. being vigilant). If these can adequately warn other members, individuals can decrease their personal vigilance level without increasing their risk of late predator detection, and spend more time on other activities such as foraging (Roberts, 1996).

The theory of selfish herding was first proposed by Hamilton (1971) and states that individuals stand a better chance of surviving an attack if they reduce their ‘domain of danger’(i.e. the area around it where a predator is closest to that individual). By putting themselves behind a conspecific, this domain decreases. In a simple model, groups became more compact due to members continually leaping to spaces between neighbours (Hamilton, 1971). Group compaction under predatory threat has been found throughout nature (Krause, 1993a, Coster-Longman et al., 2002, Viscido and Wethey, 2002, De Vos and O’Riain, 2013) providing plausible support for this theory.

Predator confusion is associated with the disorientation of predators when attempting to target a single individual among many. This creates a sensory overload, and reduces predatory success (Krause and Ruxton, 2002, Jeschke and Tollrian, 2007). In 16 of 25 studied predator-prey systems across taxa, Jeschke and Tollrian (2007) found confusion to be present in 64% of them. Some species of bird and fish attempt to enhance the confusion effect by forming compact groups and performing specialised evasive manoeuvres, such as the ‘hourglass’ or ‘vacuole’ (Eurasian minnows, *Phoxinus phoxinus*, Magurran and Pitcher (1987) and starling, *Sturnus vulgaris*, Zoratto et al. (2009)).

Grouping can further be advantageous when communal defences are considered. African ungulates for instance, form defensive formations in response to predatory threats and even attack/ mob predators (Caro et al., 2004). While an individual doing so might not win against a predator, many cooperating individuals could effectively deter predators. Mobbing predators is frequently observed in birds (e.g. Griesser and Ekman, 2005, Krams et al., 2009), and mammals (Kirkwood and Dickie, 2005, Leuchtenberger et al., 2016).

Besides anti-predatory benefits, being in a group can be advantageous whilst foraging as it offers the possibility of cooperative hunting, and an increased chance of finding food through others (Clark and Mangel, 1986). Cooperative hunting is widespread in the animal kingdom, as it can increase success rate and/or help capture prey that are too large. For instance, packs of African wild dogs (*Lycaon pictus*) have a higher hunting success, are able to tackle larger prey and increase the possibility of multiple kills per hunt (Creel and Creel, 1995); communal orb-weaving spiders (*Philoponella republican*) together reduce prey wrapping time and subdue larger prey than themselves (Binford and Rypstra, 1992). Packs of Orca (*Orcinus orca*) work together to wash prey (seals) off of ice floats (Pitman and Durban, 2012).

The chances of finding food also increase when in groups, as more individuals are looking for it (Clark and Mangel, 1986). In fish, larger shoals of guppy (*Poecilia reticulata*), goldfish (*Carassius auratus*) and minnow are able to locate food faster than those in smaller shoals (Pitcher et al., 1982, Day et al., 2001).

Being in a group can reduce the energetic expenditure of an individual. During movement, animals need to constantly overcome drag and gravitational forces, which cost energy (Vogel, 1994, Biewener, 2003). For this reason alone, many species have developed drag reducing features, such as streamlined bodies to minimize form drag (i.e. drag caused by the shape of an object) (Vogel, 1994). Formation of groups can further mitigate travel costs, as energy savings to an individual can be accomplished staying near other members, similar to how cyclists draft behind one another (McCole et al., 1990). This is of particular importance for long-distance migration. For instance, birds in flight can save energy by adapting a V-formation, and exploiting regions of upwash generated by preceding individuals. By measuring heart rate frequency, Weimerskirch et al. (2001) reports energy savings of up to 14% in a flying great white pelican (*Pelecanus onocrotalus*) group. It has shown that individual bald ibis (*Geronticus eremita*) in a V- formation indeed position themselves in optimum positions that match theoretical predictions (Portugal et al., 2014). Similarly, hydrodynamic benefits of groups of fish are based on the assumption that a diamond pattern of the school would allow for less energetic movement through (flowing) water (Weihs, 1973). Experimental work to validate Weihs' prediction has, however, yielded contradictory results, as several marine species did not take up predicted positions in shoals (Partridge and Pitcher, 1979), while another did (Partridge et al., 1983).

Whilst on the move, being in a group can, besides offering energetic benefits, also be advantageous in terms of navigational accuracy, known as the 'many wrongs principle', and decision-making. The many wrong principle states that individual navigational errors decrease as the size of the group increases (Simons, 2004). Effective navigation can further be accomplished through a limited amount of 'informed' individuals (i.e. those with directional information) are capable of guiding the rest of the group through social interactions (Couzin et al., 2005).

2.2 Costs of group formation

While factors relating to defence and foraging have been identified as the primary reason for grouping, both of these bring along costs as well. Intuitively, a group can be spotted better than an individual, and the larger the group, the higher the detection rate (Krause and Ruxton, 2002). Evidence for this has been reported from different animal taxa. Pack of wolfs (*Canis lupus*) encounter larger Elk (*Cervus* elaphus) groups more often and kill more Elk from larger groups (Hebblewhite and Pletscher, 2002). For fish, it has been shown that the larger of two guppy (*Poecilia retculata*) shoals is detected and attacked more often by blue acara (*Aequidens pulcher*) (Krause and Godin, 1995) and insects (*Daphnia* sp.) are detected faster by three-spined sticklebacks (*Gasterosteus aculeatus*) as group size increased (Ioannou and Krause, 2008).

A further cost of grouping is increased competition between group members. This is associated with foraging costs, which depend on the size of the food item or prey and the number of individuals sharing it. The bigger the group, the smaller the per capita share. As individuals compete for limited food resources, social hierarchies can form where certain subordinate individuals experience foraging costs where dominant ones benefit (Giraldeau and Caraco, 2000, Krause and Ruxton, 2002). Alternatively, food scarcity can induce kleptoparasitism, where food items obtained by certain individuals are stolen by conspecifics (Brockmann and Barnard, 1979, Iyengar, 2008).

Another important cost of grouping is an increased parasitic burden (Meunier, 2015). All members are exposed to a variety of parasites and infectious diseases, and are often in contact with or close to conspecifics. Therefore, a larger group size can be associated with higher parasitic burden. Previous research has indeed indicated a positive correlation between the two (Côté and Poulinb, 1995, Arneberg et al., 1998, Altizer et al., 2003), although collective grooming can help reduce parasite presence (Viljoen et al., 2011).

2.3 Terminology

There exists a wide variety of collective nouns used to denote a group of animals, (e.g. a group of wolves and birds are often termed a ‘pack’ and ‘flock’, respectively). For fish swimming together (relevant for this body of research), the terms ‘shoal’ and ‘school’ have traditionally been used, but interchangeably throughout the early literature. The difference between them was ultimately drafted by Pitcher (1983). He defines a shoal as a group of fish staying together for social reasons, thereby showing a significant degree of cohesion. The term school is used when fish are swimming in a synchronised manner and with a high degree of polarization (i.e. a similar orientation adopted by individuals). Schools must require some degree of cohesion for individuals to align themselves and are thus a subcategory of a shoal (Fig. 2.1A) (Pitcher, 1983, Pitcher and Parrish, 1993).

More recently, the usage of the term ‘swarm’ has been introduced (e.g. Couzin et al., 2002), to denote a large shoal without a high degree of polarization or synchronised swimming but with individuals staying in close proximity of each other. Together, the school and swarm from the extremities of shoals with intermediate forms also possible (Fig. 2.1B).

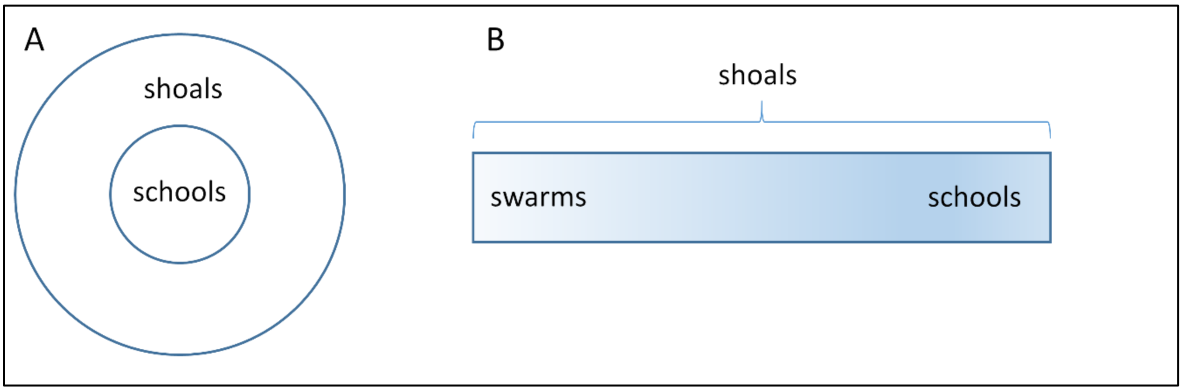

Figure 2.1. Interpretations of shoals and schools of fish. A) Early views in which schools are a subcategory of shoals. B) Extended view in which swarms are included, which fall under shoals, together with schools. Adapted from Delcourt and Poncin (2012).

Difficulties in discerning whether a group of fish is displaying swarming or schooling behaviour arise from the use of various qualitative and quantitative methods (Delcourt and Poncin, 2012). Interactions with the environment further complicate definitions. For instance, a small experimental tank can ‘force’ individuals together suggesting they shoal, where this is not truly the case. Conversely, a flow tank can induce positive rheotaxis in fish, suggesting they school. The following definitions for a shoal and school are currently postulated (Delcourt and Poncin, 2012), which, for clarity, will be used throughout this body of research:

- ‘A *shoal* is a set of individuals presenting a significant degree of cohesion, limited in a relatively small portion of space, a consequence of a social interaction between these individuals.’
- ‘A *school* is a set of individuals adopting shoaling behaviours, living in a group and adopting a significant degree of synchronisation of displacements (in speed and polarity terms) resulting from social interaction between these individuals.’

When referring to previous published work that mentions one term or another, the definition used by the authors will be used.

2.4 Self-organisation in groups

The fact that groups display effective, collective responses to perturbations (e.g. predators) and display coordinated spatiotemporal patterns indicates the presence of some form of overall order. Camazine et al. (2003) defines this as self-organization: ‘*a process in which a pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of the system.’* In this context, a pattern denotes the organised structure of individuals in space or time (Camazine et al., 2003).

Interactions at the individual level are exchanged with conspecifics and the environment (Bradbury and Vehrencamp, 1998, Couzin and Krause, 2003, Dall et al., 2005). Besides cues such as visual and olfactory ones (Bradbury and Vehrencamp, 1998), fish are able to employ a special mechanosensory organ, the lateral line (Bleckmann and Zelick, 2009, Bradbury and Vehrencamp, 1998). Consisting of a network of surface and subsurface neuromasts, the lateral line provides the fish with information on flow velocities and pressure changes from the surrounding water during locomotion (Engelmann et al., 2000, Bleckmann and Zelick, 2009).

How information is transferred between individuals and consequently leads to group patterns is an essential element in collective behaviour research (Vicsek and Zafeiris, 2012, Sumpter, 2006). The smallest entity in which social information can be transferred is a group of two individuals (Delcourt and Poncin, 2012), but since the number of individuals (and interactions) can be very large in some bird flocks or fish schools, computer models have been used extensively to capture the essence of group dynamics (e.g. Huth and Wissel, 1992, Couzin et al., 2002, Couzin et al., 2005, Hoare et al., 2004, Hemelrijk and Hildenbrandt, 2008). These models use a simple approach where each individual responds to the neighbours in a certain zonal distance around it. There are zones for attraction (far away), alignment (intermediate distance) and repulsion (close by). Using constant speed for all individuals, changes in orientation determine how information is transferred and group patterns emerge (Vicsek and Zafeiris, 2012). These simple models have led to adequate representations of group dynamics. For instance, Couzin et al. (2005) have shown that a small number of individuals with directional information can successfully lead a group with great accuracy, and Hemelrijk and Kunz (2005) have reproduced the oblong shape and high frontal density observed in fish shoals.

However, the simple approach does not allow for capturing the true dynamics of group behaviour, which follows from often more complex interactions. More recent work has attempted to overcome this knowledge gap by deriving behavioural rules directly from experimental observations (e.g. Krause et al., 2000, Ballerini et al., 2008, Cavagna et al., 2010, Katz et al., 2011, Strandburg-Peshkin et al., 2013). Some of these have already provided more detailed knowledge of the actual interaction rules used by animals. For instance, Ballerini et al. (2008) have shown that the interaction zones of European starlings (*Sturnus vulgaris*) in a flock do not meet a set metric distance from an individual. Instead, starlings react to a fixed number of neighbours. Katz et al. (2011)

have shown that in golden shiner (*Notemigonus crysoleucas*) shoals, matching of speed rather than body orientation drives fish interactions. More research is required to truly capture information transfer and self-organization in animal groups under different environmental settings.

Although experimental work has proven to aid behavioural models and vice versa, there is an important limitation to both, which is the inclusion of a lotic environment. Models assume ‘infinite space’, and experimental work has been conducted in the absence of flow (fish in standing water) or have ignored it (bird flocks). How the influence of flow could shape collective movement is particularly important for groups that experience complex flow conditions in the vicinity of barriers, experienced while migrating.

2.5 Downstream fish passage solutions

Research into downstream passage has received considerable less attention compared to that involved with upstream passage (Larinier and Travade, 2002, Williams et al., 2012). For instance, the first attempts to aid upstream migrating fish past anthropogenic barriers were developed in Europe in the 18th century (Clay, 1995), and consisted of types of fishway (i.e. a structure on or around the barrier. Downstream passage at the time was often ignored, because the losses did not seem to affect numbers of returning adults the following year. When these started to decrease, it was realised that more effort was required to protect downstream migrants (Katopodis and Williams, 2012).

Negative impacts of barriers on downstream migrants include migratory delay and associated predation pressure, damage and mortality as a result of passage through hazardous routes of intakes such as turbines, irrigation channels or spillways (Čada et al., 1997, Blackwell and Juanes, 1998, Larinier and Travade, 2002, Marschall et al., 2011). In turbines, injury or death may follow from contact with blades and turbine infrastructure, pressure changes affecting the swim bladder, or disorientation due to turbulence (Coutant and Whitney, 2000, Ferguson et al., 2006, Schilt, 2007). At irrigation intakes, entrained fish can be trapped and perish if no return route is available (Baumgartner et al., 2009). Via open spillways, fish are injured by contact with hard surfaces, subject to changes in velocity, turbulence and pressure after falling down from considerable heights, or possibly exposed to dangerous gas-supersaturated water downstream (Elder et al., 2016, Larinier and Travade, 2002).

Efforts to mitigate for the negative impacts for downstream migrants have primarily focused on measures that primarily aim to prevent fish from entrainment and, secondarily, guide them to a safe alternative route. They can be broadly categorised into behavioural barriers and physical screens (Larinier and Travade, 2002, O'Keeffe and Turnpenny, 2005). Behavioural barriers act by creating a stimulus that elicits a behavioural response by the fish and consequently deters them. Examples include usage of air bubble curtains (Fig. 2.2A), sound, illumination, or a combination of both (Taft, 2000) (Fig. 2.2B). Louvers are a combination of a behavioural and physical screen, and operate by creating local areas of high turbulence between individual slats of the louver. The resulting turbulent shearing flow is avoided by fish and guides them towards a bypass (Odeh, 1999). Physical screens are more commonly used, and are structures implemented in the waterway that allow water to pass through but exclude fish. A variety of these have been developed, including panelled screens, trash and bar racks, submerged travelling screens, rotating drum screens, and Coanda screens (O'Keeffe and Turnpenny, 2005). Panelled screens are usually made of mesh or wedge-wire (i.e. triangular shaped wires welded onto support bars) and slotted into a frame to cover a larger surface area (Fig. 2.2C). Trash racks are often present near intakes to block debris but serve a screening purpose as well (e.g. Greenberg et al., 2012). Similar to bar racks, they consist of an array of vertical bars in a supporting frame (Fig. 2.2D). Submerged travelling screens are usually found at large hydropower plants and divert fish upwards to surface collection channels instead of entering turbines. Rotating drum screens are circular in shape and rotate due to local water flow while blocking fish entry (Fig. 2.2E). Coanda screens are specifically designed for curved surfaces, such as those of weirs, and allow for water to fall through while fish drift over (Fig. 2.2F).

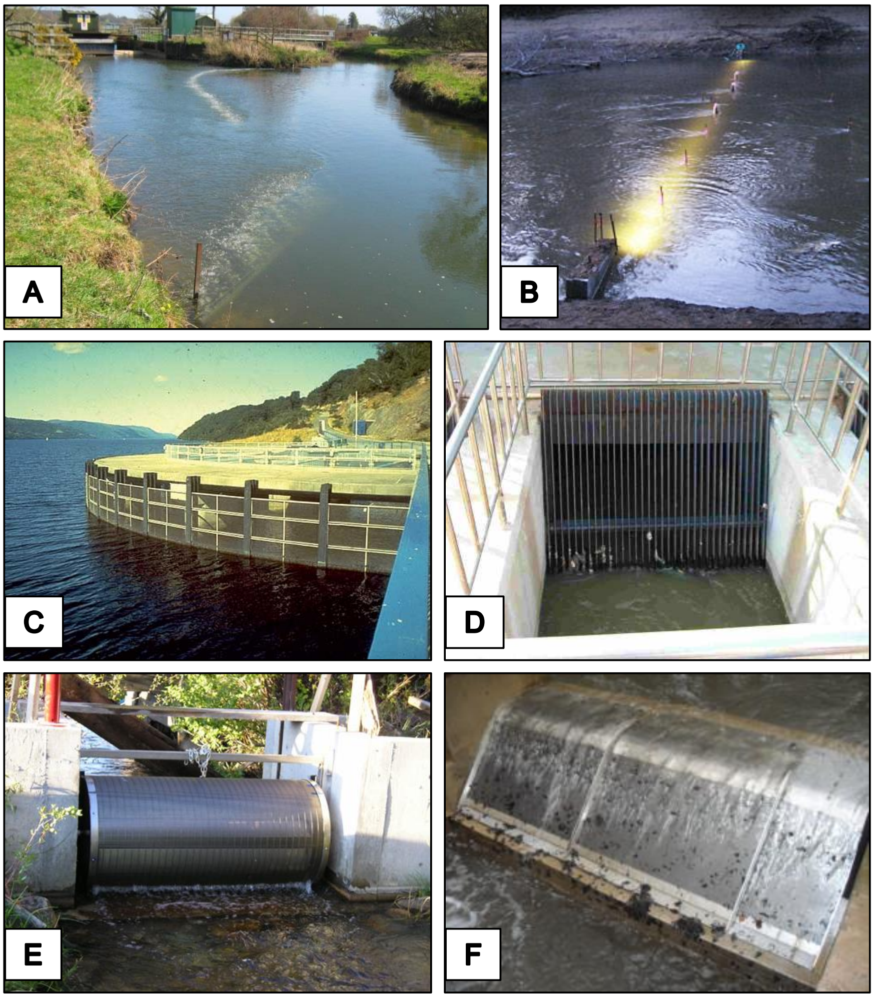

Figure 2.2. Examples of behavioural and physical screens: A) bubble curtain, B) combined sound and strobe light screen, C) mesh panel, D) trash rack, E) rotating drum screen, and F) Coanda screen.

2.5.1 Design Criteria

The design of any fish screen should be such that the potential for their functioning is optimal. For this reason, criteria have been imposed, primarily associated with providing an escape route and suitable hydrodynamic conditions that minimise entrainment/ impingement for the species under consideration; and ensure guidance into a bypass, while minimising head losses over the screen (Clay, 1995, Turnpenny et al., 1998, McMichael et al., 2004).

Firstly, if a screen is oriented perpendicular to the oncoming flow, there is no escape route provided to fish and high numbers of entrained or impinged fish can be expected. Therefore, screens should either be angled towards the flow (horizontally) with a bypass located at the downstream end. Alternatively, it can be vertically inclined with a bypass located close to the surface (Larinier and Travade, 2002, Calles et al., 2013).

Secondly, fish should be able to actively prevent themselves from contact with screens and/ or from entrainment. In this context, certain flow velocity criteria have been prescribed to ensure that the targeted fish species' swimming capabilities can overcome them (Turnpenny et al., 1998). The mean flow velocity (V), as it approaches the screen, can be decomposed into two components (Fig. 2.3). The sweeping velocity (V_s) is defined as the component parallel to the screen, and the escape velocity (V_e) as the one perpendicular to it (Pavlov, 1989, EPRI, 1998). The angle towards the oncoming flow should therefore be ≤45° so that the sweeping velocity exceeds the escape velocity and reduces entrainment (Larinier and Travade, 2002). The magnitude of the escape velocity should suit the species of consideration, and threshold velocity criteria are in place to ensure this (e.g. 30 cm s^{-1} for salmon and trout smolts) (Turnpenny et al., 1998). However, V is diverted by the presence of the screen, with consequences for the magnitude of both the sweeping and escape component (Fig. 2.3).

Finally, with the bypass located at the downstream end or towards the surface, the flow conditions near its entrance are critical for the efficiency of screens. The velocity gradient along the screen should gradually increase towards the bypass, and areas of high turbulence avoided (Larinier and Travade, 2002).

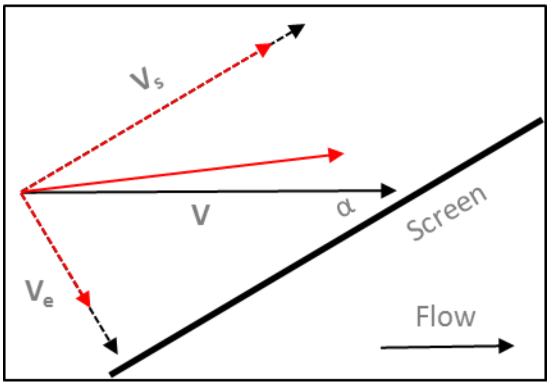

Figure 2.3. Velocity components in front of a screen. Mean velocity vector **V** can be decomposed in to a sweeping (**V$_s$**) and escape (**V$_e$**) component (black arrows). Close to the screen, **V** changes direction due to the presence of it, with consequences for the magnitudes of **V$_s$** and **V$_e$** (red lines).

The characteristics of the screens themselves can influence local hydrodynamic conditions and affect guidance (Katopodis et al., 2005). Previous studies have investigated how different screen configurations, their bar shape and size influence head losses and velocity distributions along them (e.g. trash racks, Raynal et al., 2013a, 2013b, Tsikata et al., 2014, barrier screen, Hughes et al., 2011, wedge-wire screen, Katopodis et al., 2005, Rajaratnam et al., 2010, and louver, Shepherd et al., 2007). Head losses of any screen are linked to the drag force $\boldsymbol{F_d}$ (equation 7.1).

$$F_d = \frac{1}{2}\rho u^2 C_d A. \tag{2.1}$$

where $\boldsymbol{\rho}$ is density, $\boldsymbol{u}$ is the oncoming flow velocity, $\boldsymbol{C_d}$ is the drag coefficient, and $\boldsymbol{A}$ is the blockage area. The drag force can be measured with e.g. load cells under variable values of $\boldsymbol{u}$ and $\boldsymbol{A}$, and allows for determination of the drag coefficient. This information can help determine which screen would produce the lowest head losses under certain field conditions and thereby establish fish-friendly swimming criteria while minimising these. A possible improvement in this context is the usage of horizontal bars rather than vertical ones in traditionally used bar and trash racks (Ebel, 2008, Ebel et al., 2015).This is supposedly for three reasons: 1) due to the aspect ratio of most fish (they are higher than wide), contact to a horizontal bar screen occurs with wider bar spacing than with vertical bars. This reduces head losses while the same fish are still screened (Horsfield and Turnpenny, 2011); 2) fish are less limited in their body movements when impinged between horizontal bars, and they can presumably escape or better prevent being entrained; 3) horizontal bars facilitates cleaning and maintenance, as debris can be removed in the flow direction rather than upwards (Ebel et al., 2015). So far, a direct comparison between the two configurations has not been made to validate the above assumptions, and offers possible opportunities for screening research.

2.5.1.1 Costs of screening systems

Many different forms of legislation have been put into place (Kemp, 2016) to enforce screening at intakes. Depending on total screened area, discharge level and other local site characteristics, screens can cost thousands of pounds/ dollars. Bar racks for example can cost up to £250k, and this excludes installation and maintenance costs (O'Keeffe and Turnpenny, 2005). A cost-effective approach should be taken when it comes to screen design.

2.5.2 Evaluation of screen performance

Studies on the efficiency of screening systems have not been conducted as much as those for fish passes (Noonan et al., 2012, Bunt et al., 2012, Roscoe and Hinch, 2010). Despite this general lack of evaluation studies of screen efficiency, (Moyle and Israel, 2005), useful attempts have been made through the calculation of Fish Guidance Efficiency (FGE) (Ploskey and Carlson, 1999, Scruton et al., 2003). This is defined as the number of guided fish as proportion of the combined numbers of guided and unguided fish. Although FGE calculations are useful, they merely represent the outcome, and do not take into behavioural traits (such as avoidance responses and delay) that precede guidance. In the field, FGE can best be generated using telemetric methods such as Passive Integrated Transponder (PIT) tags, radio transmitters or acoustic telemetric transmitters (Cooke and Hinch, 2013), whereas lab studies can make use of untagged fish and video recordings.

Numerous studies have calculated FGE under both laboratory and field settings. Flume studies with American eels (*Anguilla rostrata*), find efficiency ranges between 56.8% and 95.2% of bar rack and louvers under various screen angles and discharge levels (Amaral et al., 2003). Russon et al. (2010) reports a FGE >98% for European eels (*Anguilla anguilla*) encountering angled bar racks in a flume. Field studies with eels on the other hand report FGE estimates from 0% (Calles et al., 2012), between 56-64% (Gosset et al., 2005), 82% (Calles et al., 2013) to over 89% (Inglis et al., 2016) under different settings across Europe.

For salmonids, estimates of FGE come exclusively from field experiments with tagged individuals. A seven-year (1983-89) monitoring programme on the Bonneville Dam (Columbia River, USA) indicates FGE <33% of submerged travelling screens for chinook (*Oncorhynchus tshawytscha*) coho (*O. kisutch*) and steelhead (*O. mykiss*) smolts in 1983 that increased to around 70% in the following years after modifications to the screen and intakes were made (Gessel et al., 1991). A three-year programme on a different (Wells) dam on the Columbia River shows a FGE range of 84.3-95% and 76.5-97% for spring and summer migrating sockeye salmon (*Oncorhynchus nerka*) smolts (Skalski et al., 1996). A five-year programme (1997-2001) reports initial FGEs of <25% for Atlantic salmon (*Salmo salar*) smolts the first two years, but after modification of the louver system, reports increased values to 54%, 65.3% and 73.3% in following years

(Scruton et al., 2002, 2003). Chanseau et al. (1999) reports an increase from 17% to 55% after installation of a training wall to aid trash racks in Atlantic salmon smolt guidance in France. Across four other sites in France, trash racks yield a mean FGE between 32.3% and 70.9% at four hydropower plants (Croze, 2008), and bar racks 17% at a plant in Sweden (Calles et al., 2012). In the UK, wedge-wire screens can have a FGE > 87% (Inglis et al., 2016) for this species.

Data on screen efficiency for species other than salmonids/ eels is scarce. For instance, bar racks and louvers can be 70% efficient under certain conditions for seven species, including endangered lake and shortnose sturgeons *Accipenser fulvescens* and *A. brevirostrum*, (EPRI, 2001, Amaral et al., 2002). Wedge-wire screens can achieve up to 40% FGE for juvenile splittail (*Pogonichthys macrolepidotus*) (Danley et al., 2002).

The above studies and others (e.g. Scruton et al., 2007, Evans et al., 2008, Wertheimer, 2007, Mussen et al., 2015) strongly suggest that evaluation of screen efficiency is biased towards economically important, diadromous fish species (Williams et al., 2012, Kemp, 2016). It is further clear that there a lot of variability exists in the obtained efficiencies, and that a standard of 90% is not often obtained. Given the large variation of screens, their characteristics e.g. bar rack spacing varied from 10mm (Russon et al., 2010) to 50mm (Amaral et al., 2003), and flow conditions in the described studies, valid comparisons of efficiencies are difficult to make. However, since many screening systems do not perform optimally, it is important to generate more knowledge on factors that limit screen functionality, and ways to improve this.

2.5.3 Factors limiting efficiency

Data from experiments on swimming capabilities of fish was initially used to prescribe suitable approach velocities for screening purposes (Clay, 1995). However, since then, experimental work has shown that near screens, fish often do not perform optimally

(Swanson et al., 1998, 2004). If escape and sweeping velocities are too high, unwanted contact with the screen surface and associated injury/ mortality often occurs (Swanson et al., 2004, White et al., 2007, Calles et al., 2010, Boys et al., 2013). Some species, such as splittail (*Pogonichthys macrolepidotus*), are capable of adapting their swimming speed under increasing velocity treatments to minimize screen contacts (Danley et al., 2002). European/ American eels on the other hand may only react after contact and are thus prone to injury (Brown et al., 2009, Russon et al., 2010).

Accelerating of flow near the screen as well as close to the bypass entrance may elicit an avoidance response (positive rheotaxis followed by rejecting the area) that can delay passage. Such a response has been observed for solitary European eels (Gosset et al., 2005), groups of Atlantic salmon smolts (Larinier and Travade, 1999) and American shad, *Alosa sapidissima* (e.g. Kynard and Buerkett, 1997). Other studies have demonstrated that individual European eels (Piper et al., 2015), groups of Pacific salmonid smolts, *Oncorhynchus sp.* (Kemp et al., 2005, Enders et al., 2009) and individual trout (Vowles et al., 2014) display the same avoidance response to areas of accelerating flow not created by a bypass. This suggests that the nature of such a response is intrinsic and not limited to screens leading to a bypass.

Basic behavioural preferences can also affect screen functioning. Eels for example are benthic species that prefer to stay to the bottom during migration (Brown et al., 2009), whereas salmonid smolts tend to form groups and be surface oriented during migration (Coutant and Whitney, 2000, Gosset et al., 2005). This suggests that different bypass locations are required for different species.

The preference of fish species to shoal has received little to no attention in the context of screen guidance so far, despite a number of laboratory screen studies that used more than one individual per trial (e.g. Kynard and Buerkett, 1997, Danley et al., 2002, Young et al., 2010). Only one study to date has specifically compared downstream moving groups to individuals, when released upstream of a screen (Lemasson et al., 2014). They report that juvenile palmetto bass (*Morone chrysops* x *M. saxatilis*), show a 23-fold increase in residence time at a louver screen when in groups compared to as individuals. This is due to the group's passive movements (oriented against the flow), as opposed to individuals who face downstream and quickly enter the bypass (Lemasson et al., 2014). The delay groups can thus incur could enhance risk exposure through predation or fatigue.

The role of hydrodynamics in the performance of fish screens is clearly established. Interspecific differences in behaviour to hydrodynamics clearly determine whether entrainment or successful guidance occurs, and therefore overall screen efficiency. To better mitigate the impact of screens on fish shoals, which is currently lacking, an understanding of the basic collective fish response to hydrodynamics is required.

2.6 Fish behaviour and hydrodynamics

Not only near intakes, but throughout riverine systems, the presence of a range of hydrodynamic conditions is ubiquitous (Allan and Castillo, 2007). Moving through (flowing) water induces drag on a fish's body, which affects their ability to navigate through this medium. To minimize energy expenditure, fish have evolved different ways that minimize form drag, e.g. by having a streamlined body, and skin friction, e.g. by secreting mucus (Vogel, 1994). Streams are furthermore very complex in nature, and usually contain a certain degree of turbulence (i.e. vortical flow (eddies) of varying intensity and magnitude, superimposed on the mean flow velocity) (Hawkins et al., 1993).

Studies have investigated fish distributions in natural conditions in relation to mean flow velocity or turbulence level. Ontogenetic shifts to faster flowing water have been observed, for example in four cyprinid species (Watkins et al., 1997) or Cape Fear shiners (*Notropis mekistocholas*) (Henderson and Johnston, 2010), and is for reasons of reduced predation, food availability or lower competition. Various other studies demonstrate that certain flow velocities are preferred within an available range, e.g. for silver shiners (*Notropis photogenis*) (Bunt, 2016); minnows (*Phoxinus phoxinus*) (Garner, 1997); brown trout (*Salmo trutta*) (Campbell and Scott, 1984), and rainbow trout (*Oncorhynchus mykiss*) (Dauwalter et al., 2014). A recent long-term study with Atlantic salmon (*Salma salar*) redds showed that yearly variation in flow in the river Frome (UK) affected redd distribution, with adverse effects for reaching suitable spawning grounds (Parry et al., 2017).

Both field and lab studies have shown that the level of turbulence affects fish swimming, energetic costs and distribution (e.g. Pavlov et al., 2000, Enders et al., 2003, Lupandin, 2005, Tritico and Cotel, 2010), although sometimes inconclusive (Nikora et al., 2003). For a number of cyprinid species, Pavlov et al. (2000) report that an increase in turbulence decreased overall swimming performance (e.g. in terms of sustained swimming speed which can be maintained for over 200 mins), and that fish selected certain zones depending on their needs (for instance, starved fish selected more turbulent zones to increase foraging success). Respirometry experiments have related turbulence level to swimming costs (Enders et al., 2003, 2005). Turbulence seems to affect swimming performance of fish when the diameter of its turbulent eddies exceeds 2/3 of the fish's body length, as demonstrated in perch (*Perca fluviatilis*) of three different size groups of 30-60, 61-90, and 91-120 mm body length. Adjusting fin position to stabilize their body, perch suffered a decrease in swimming speed (Lupandin, 2005). Tritico and Cotel (2010) further report that horizontal oriented eddies destabilize creek chub (*Semotilus atromaculatus*) swimming more than a vertical ones due to the fish's fin morphology. In the wild, fish have been found to select certain areas in rivers, related to the amount of turbulence experienced (Shtaf et al., 1983, Skorobogatov et al., 1996, Pavlov et al., 2000, Cotel et al., 2006). Furthermore, fish have developed specialised behaviours to exploit turbulent flows generated by in-stream objects for holding station and saving energy (Liao, 2007). For instance, river chub (*Nocomis micropogon*) and smallmouth bass (*Micropterus dolomieu*) entrain behind horizontal and vertical cylinders (Webb, 1998), rainbow trout (*Oncorhynchus mykiss*) near D-section cylinders display bow-riding, entraining or exploiting periodic shed vortices, called Kármán gaiting and decrease swimming effort (Liao et al., 2003a, Liao et al., 2003b). Recently, two additional behaviours, wall and tail holding, have been identified in brown trout (*Salmo trutta*) for holding station over a prolonged period (Kerr et al., 2016). It thus seems that fish distribution in lotic environments is determined by fish attempting to minimize energy expenditure (Facey and Grossman, 1992).

Experimental research that investigated collective behaviour in response to flow under controlled conditions is scarce. This is surprising given that flow is ubiquitous in natural rivers. Pitcher (1973b) investigated the three-dimensional structure of minnow (*Phoxinus phoxinus*) schools under varying discharge, reporting that school structure does not follow a clear pattern and breaks up under high (> 0.125 m s^{-1}) flow. Chicoli et al. (2014) investigated how school structure, threat detection and response rates varied between groups of giant danio (*Devario aeguipinnatus*) under flowing compared to standing water. Results show that school structure under flow expanded in the crosswise direction, and that threats were detected better in flow. Hockley et al. (2014) compared aspects of shoaling (e.g. cohesion and time spent shoaling) between infected guppies (*Poecilia reticulate*) under flow and standing water. Results show that larger shoals formed in standing water, and that infected fish influenced shoal structure structure more under flow than standing water. Recently, (Hansen et al., 2016) investigated the spatial position of starved rainbowfish (*Melanotaenia duboulayi*) in shoals of eight individuals under flowing conditions. Results show that starved individuals are often in the front of the shoal where more food items can be obtained.

Most experimental studies on shoaling behaviour under flowing conditions have investigated how energetic benefits can be accomplished when swimming together. This was hypothesised to be possible early on, by suggesting that fish's body movements would shed vortices that could be exploited by trailing conspecifics (Belyayev and Zuyev, 1969). A more detailed theory was developed a few years later (Weihs, 1973). Assuming infinite large schools, members of the same size and fish swimming with the same speed, an individual should swim midway behind two preceding fish that swim next to each other, to exploit their thrust wakes which generate a reverse Kármán vortex street (Fig. 2.4). Furthermore, fish swimming could benefit from the presence of lateral neighbours by mutual exploitation of oscillatory body movements in a synchronized manner, called a channelling effect. In doing so, the thrust produced by each fish can be increased by tens of percentages without a change in energy expenditure. Finally, vortices produced by pectoral fins could provide updraft (lift) for trailing fish. The resulting pattern would be a 'diamond lattice' in the horizontal plane (Weihs, 1973).

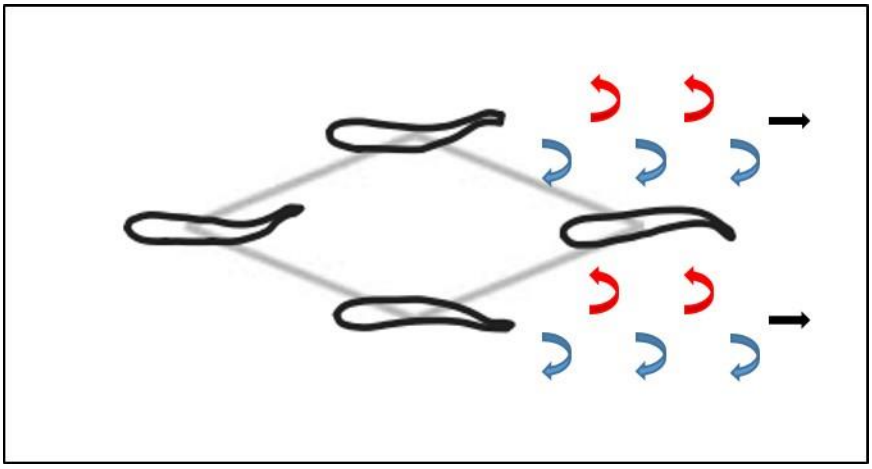

Figure 2.4. Hypothetical diamond pattern of schooling fish that would optimize energy savings. Swimming movements of two fish side by side create vortices (red and blue arrows) that together create a reverse Kármán vortex street, which can be exploited by a trailing individual. Modified from Liao (2007).

Experiments and numerical simulations with biomimetic foils (mimicking fish) have provided a good understanding of the interactions between fish and surrounding fluid (Triantafyllou et al., 2004, Wang et al., 2016). For the most simple case of two interacting foils, hydrodynamic benefits can be provided for the trailing foil, when in tandem configuration (i.e. one foil leading the other) (Akhtar et al., 2007, Boschitsch et al., 2014). Depending on the distance between them, and the phase difference in their oscillating movements, the trailing foil can enhance both thrust production and propulsive efficiency (Boschitsch et al., 2014). This has also been found in a case mimicking the dorsal-caudal fin interactions of a single fish (Akhtar et al., 2007). For two interacting foils in a side-by-side configuration, overall performance is best during in-phase compared to out-phase oscillations, with greatest propulsive efficiency (at the cost of thrust-production) in this case (Dewey et al., 2014). Similar results have been obtained for more foils in this configuration (Dong and Lu, 2007, Bergmann and Iollo, 2011). For configurations with more than two foils, numerical studies have confirmed that individuals situated laterally in between two preceding fish can indeed benefit from their wake, in terms of increasing propulsive efficiency (Deng and Shao, 2006) or reducing flapping frequency (Wu and Wang, 2010).

Experimental observations on real fish schools do not fully support Weihs' theory of energy savings mechanisms. Schools of saithe (*Pollachius virens*), herring (*Clupea harengus*) and cod (*Gadus morhua*) did not adhere to the predicted structure and did not create the correct vortex streets (Partridge and Pitcher, 1979). Conversely, schools of Atlantic Bluefin tuna (*Thynnus thynnus*) adopt a beneficial structure whilst hunting (Partridge et al., 1983); and blackfin shiner (*Notropis heterodon*) schools change their hydrodynamic flat configuration by expanding in the vertical when a predator is present to enhance detection (Abrahams and Colgan, 1985, 1987).

The best evidence for a hydrodynamic advantage of schooling comes from experiments focused around measurements of energetics of schooling fish. Metabolic rate (MO_2) and Tail Beat Frequency (TBF) are commonly used metrics in such work. It has been shown that TBF was significantly lower in sea bass (*Dicentrarchus labrax*) (9-14%), roach (*Rutilus rutilus*) (7.3-11.9%) (Herskin and Steffensen, 1998, Svendsen et al., 2003). Grey mullet (*Liza aurata*) at two different flow velocities have lower TBF when trailing others compared to leading them (at 20 cm s^{-1}: 1.75+0.05 Hz vs. 2.00+ 0.05 Hz; at 30 cm s^{-1}: 2.08+0.07 Hz vs. 2.35+0.09 Hz) (Killen et al., 2011), indicating these fish spent less energy to maintain position. Burgerhout et al. (2013) reports reduced TBF (2.6 ± 0.1 vs. 3.8 ± 0.1) and oxygen consumption rates (21.3 ± 3.2 vs. 32.0 ± 0.6 mg O_2 kg^{-1} h^{-1}) in schooling eels (*Anguilla anguilla*) compared to individuals. In a recent study it has been shown that an individual grey mullet at different positions in a school had a reduced TBF up to ± 30% and a reduced metabolic rate up to 19.4% compared to a single individual swimming at the same speed (Marras et al., 2015).

In summary, there seems to be evidence that schooling in a specific structure offers energy savings for individual members. The above approaches however have neglected to investigate whether fish are actively seeking these positions in a school. It is unclear whether energy savings are an actual driver of fish schooling and a specific trait of fish behaviour. Analysis of interaction rules under flowing conditions offers a possibility to answer this, as compared to standing water a flow field induces higher energy expenditure for fish and therefore encourages energy saving through adaptive schooling. Interaction rules between fish have not been investigated in the context of a flow field, only in standing water (Herbert-Read et al., 2011, Katz et al., 2011). There appears to be a knowledge gap in the detailed understanding of how collective fish behaviour emerges under influence of flow. Further research into this is warranted, as it could aid in development of suitable flow conditions near screening systems.

2.7 Summary

Through completion of the literature review, it can be concluded that knowledge of the benefits and costs of living in groups has been well established (Krause and Ruxton, 2002). The functioning of groups is highly dependent on adequate member interactions and information transfer between them (Vicsek and Zafeiris, 2012). While extensive modelling of collective behaviour has been conducted, studies that derive interaction rules directly from observations aid in the accuracy of them (e.g. Katz et al., 2011).

Habitat fragmentation caused by human exploitation of water as a natural resource calls for adequate mitigation for adverse effects on freshwater migratory species (Clay, 1995, Odeh, 1999). Fish passage research has traditionally focused on upstream migrants, and economic important, diadromous species such as salmonids (Katopodis and Williams, 2012). Protecting downstream migrants is commonly accomplished by installation of behavioural barriers (that deter fish by exploiting their senses) or physical screens, that block entry into intakes and divert fish to a safe bypass route (Larinier and Travade, 2002). Many fish species form groups at some point in their life cycle, mostly as juveniles (Shaw, 1978). Being less developed than fully grown adults, shoals of juveniles are particularly susceptible near intakes, and effective screening solutions are required.

Physical screens often perform not to a very high standard, and their efficiency has again been predominantly assessed for diadromous species. Behaviour rather than swimming capabilities is a key factor in screen performance (Williams et al., 2012). An interdisciplinary approach that combines the design (field of engineering) and evaluation (field of biology/ ecology) is required to improve passage (Odeh, 2000, Katopodis and Williams, 2012, Williams et al., 2012). Many fish species migrate throughout riverine systems (Lucas and Baras, 2001), and a better understanding of the behavioural response of the wider fish community to the hydrodynamic conditions encountered at screens will improve mitigation strategies. This research will benefit from studies that investigate the fundamental response of single-species fish shoals under lotic conditions.

To date, research on collective behaviour in response to flow has predominantly focused on the energetic benefits of being in a group, but have not yet determined whether that is an important driver for shoaling. Interaction rules of single species shoals under lotic conditions have not extensively been investigated and will aid in prescribing suitable hydrodynamic conditions that facilitate downstream movements of shoals past screens. The following research objectives are thus established (Fig. 2.5):

ii. Quantify the behavioural response of shoaling fish to controlled flow conditions.

iii. Quantify hydrodynamics associated with different types and configurations of fish screens.

iv. Quantify the performance of these fish screens for guiding groups of potamodromous fish.

v. Determine the behavioural response of these species to screens and associated hydrodynamics in the context of the observed performance.

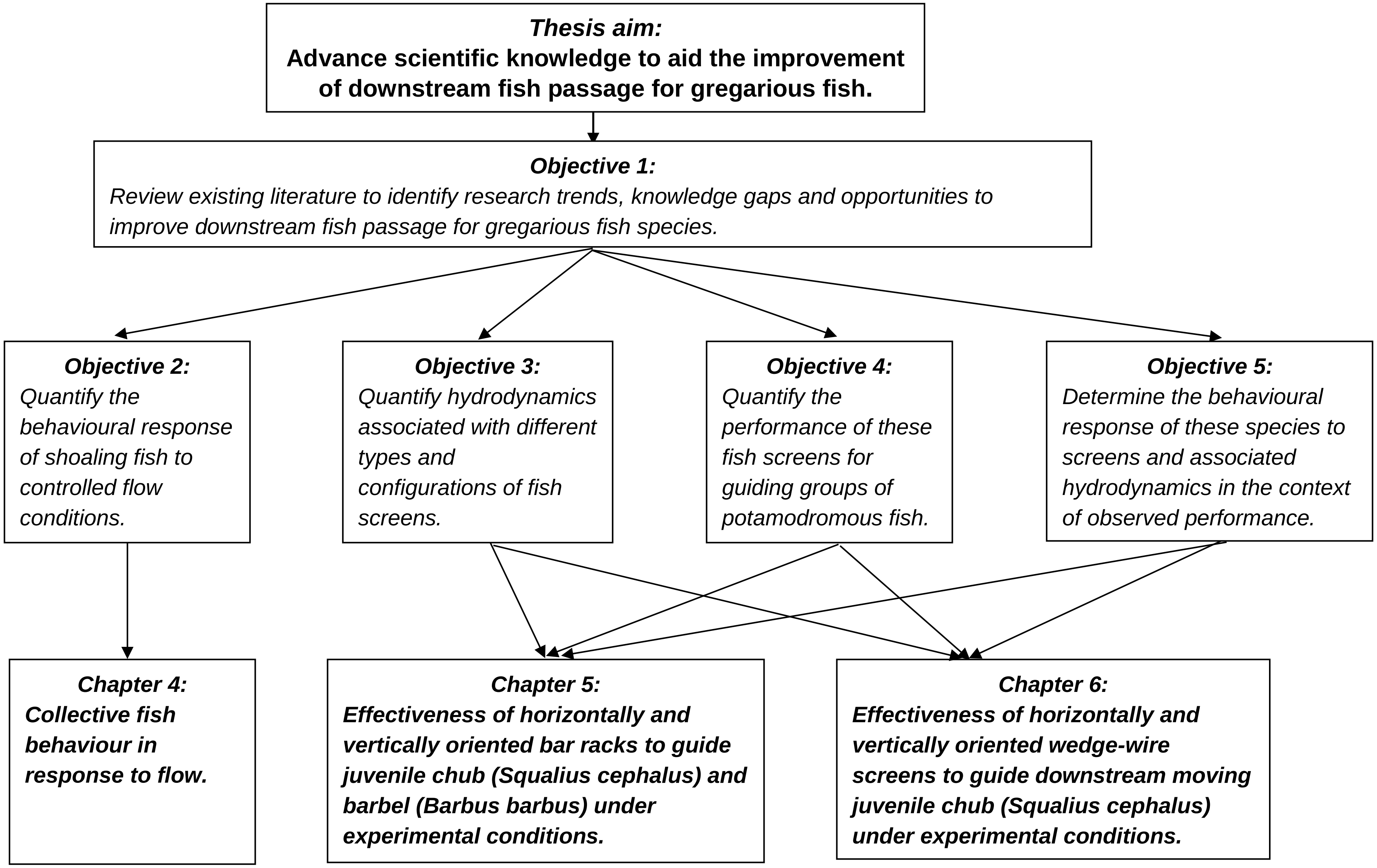

Figure 2.5. Schematic overview of the thesis aim and objectives with corresponding results chapters.

Chapter 3: General Methodology

In this chapter, a justification for the usage of flumes is presented, followed by a description of general aspects of methodology techniques used throughout experimental research conducted for this thesis. Additional details on methodology are presented in each results chapter separately.

3.1 Flume facilities

Both laboratory flume experiments (e.g. Kerr et al., 2016) and field studies (e.g. Piper et al., 2015) have been used to study fish behaviour in response to hydrodynamics, and there are advantages/ disadvantages to both. Firstly, flume studies allow for consistent control of certain variables, whilst others can be manipulated and clear relationships between them can be established. (Rice et al., 2010). In the study by Kerr et al. (2016) for example, discharge was controlled to create a consistent, heterogeneous hydrodynamic environment throughout trials to assess space use by brown trout (*Salmo trutta*), while visual cues were eliminated using polyurethane sheets around the experimental area. Secondly, experiments can be easily replicated under the same circumstances when performed in a laboratory, which is invaluable for statistical testing. However, such experiments come at the cost of *in situ* validity (Rice et al., 2010). Natural environments are usually much more complex and influenced by many confounding variables, which makes the extrapolation of measured fine-scale fish movements from laboratory to field conditions a challenge. Field studies usually employ acoustic telemetry techniques to monitor fish behaviour and the advancement of this technology will help towards bringing together laboratory and field results (Hellström et al., 2016). For the scope of this research, consistent control over important flow variables as well as the possibility of gathering statistical sound behavioural data justified the usage of flumes over field experiments. Procedures towards recreating the natural conditions under which represent the test fish display their natural behaviour included minimising stress to fish during transport to experimental facilities, careful acclimating to holding tank and flume water temperature and chemistry, and undertaking trials under light conditions when fish are most likely to form shoals (Shaw, 1978).

Throughout this body of research, experiments were undertaken in two recirculating flumes, based at the International Centre for Ecohydraulics Research (ICER) facilities at the University of Southampton, UK (50°56’7.8” N, 1°23’34.0” W & 50°57’42.1” N, 1°25’26.8”W). The first flume has a working length of 12.00 m, width of 0.30 m and height of 0.50 m (Fig. 3.1A). It has glass sided walls, a solid concrete base and is driven by one centrifugal pump (capacity 0.03 $m^3 s^{-1}$). Discharge is controlled by a valve on the pipe that recirculates water underneath the flume. Flow depth can be controlled by adjusting a blocking weir at the downstream end. The second, large indoor flume has a working length of 21.40 m, width of 1.39 m and depth of 0.60 m (Fig. 3.1B). It has glass sided walls, a solid concrete base and is driven by three centrifugal pumps (capacities 0.09, 0.15 and 0.23 $m^3 s^{-1}$, respectively) providing a combined, maximum discharge of 0.47 $m^3 s^{-1}$. The three pumps can be controlled independently of one another, and different discharge regimes could thus be established. Water depth in the flume can further be controlled by adjusting an overshot weir at the downstream end of the flume. Both flumes could be fitted with different structures to create specific experimental conditions (e.g. squared mesh panels to isolate a section in it, Chapter 5) and secured either directly to the flume walls/ floor or by attaching them to a railing (Item, Industrietechnik, Germany) that ran along the sides of the flumes.

Figure 3.1. Recirculating flumes at the ICER facility used in this research: A) 12.0 m long indoor flume, B) 21.4 m long indoor flume.

3.2 Video analysis and tracking

Experimental trials were video recorded from above using overhead mounted cameras (Casio EXILIM EX-F1 [Chapter 5], and AV-TECH Sony Effio 580TVL and Swann PRO-735 TVL CCD, [Chapter 6- 7]). Some aspects of fish behaviour (e.g. discrete counts of avoidance behaviour) could be directly extracted from watching back the footage using split-screen video playback software (NUUO Inc., Taiwan). Analysis that required more detailed information (e.g. trajectories) required video footage to be tracked on a frame-to-frame basis (29.97 fps). This was accomplished using the free tracking software Ctrax (0.5.2), which uses the contrast between fish and background to determine its position and orientation through consecutive frames. The tracking output was manually checked for errors using the Matlab (R2012a) ‘Fixerrors’ toolbox. Common tracking errors after the automated process included the loss of identity when individuals crossed over each other and orientation switches of individuals, which could easily be corrected.

3.3 Hydrodynamics

At the start of every day of trials, consistency of discharge levels from pumps was checked by measuring the resulting flow velocities at the beginning of the experimental area. These measurements were taken perpendicular to the flow at 50% depth. Velocity measurements were acquired using an electromagnetic flow meter (Valeport Ltd., model 801). This device was pre-set to record velocities over ten seconds and presented the mean velocity and corresponding standard deviation. For fine-scale flow measurements, a Nortek Vectrino+ Acoustic Doppler Velocimeter (ADV) was used. The ADV allows for 3D velocity data to be collected at each selected measurement point. The apparatus emits acoustic pulses and measures the change in frequency upon return of the pulse. In this research, sampling volume was 0.28 cm^3, and sampling frequency was set to 50 Hz for a duration of 60 s. As a result, 3000 discrete velocity measurements were taken at each point. Raw ADV data was filtered using the protocol described by Cea et al. (2007), before further processing and plotting in Matlab.

3.4 Fish husbandry and handling

If sufficient numbers could be obtained, experimental fish were caught in the wild; otherwise they were sourced from a fish farm in Calverton, UK (53°2’1.3” N, -1°3’7.0” W). By using hatchery-reared fish for scientific purposes, the natural population remains unaffected, which is particularly important for species that are not abundant or where juvenile life-stages are concerned. However, previous research has shown that hatchery-reared fish perform less well compared to wild fish in terms of swimming capabilities and fitness (essential in this body of research), e.g. in salmonids (Enders et al., 2004, Pedersen et al., 2008, Chittenden et al., 2010). In order to prevent fish from adapting to the experimental setup (i.e. using each fish only once), while aiming to reach statistical validity a sufficiently high sample size was required. For two species under consideration, hatchery-reared individuals were thus sourced from the fish farm. This should be considered when evaluating the results from this research.

Fish from the wild were caught using a seine net (3 m long, 5x5 mm aperture size) and transported in aerated river water into four 100 L holding tanks with dechlorinated, oxygenated water at the ICER facility (Fig. 3.2A). Farmed fish were transported in plastic bags with oxygenated (over-saturated) water and maintained in four 3000 L holding tanks with dechlorinated and oxygenated water at the ICER facility. Each of these tanks was equipped with its own filtration systems, including an UV filtration system (Fig. 3.2B). Before release into holding tanks, fish were acclimatised to their water temperature over the course of two hours. No fish died as a result of the transport and acclimation time. Water quality (levels of NO_3^-, NO_2^-, NH_3 and pH) was monitored daily and where necessary, 50% water changes were carried out. Water temperature in holding tanks and flumes were monitored with HOBO UA-002-08 Data loggers (ONSET, USA). All trials started at least two hours after feeding, and fish were acclimatised to indoor flume temperatures prior to usage. If the difference in water temperature between holding tanks and flume exceeded 2°C, a trial was not undertaken.

Experimental fish were carefully measured and weighed after each trial. Measurements included the total length measured from the tip of the snout to the tip of the caudal fin (TL), and the body length measured from the tip of the snout to the posterior end of the last vertebra (BL). As measurement procedures took little time (less than 30 s) it was deemed unnecessary to euthanize test fish for this specific reason. No fish was injured or died as a consequence of the measurement procedure. After trials, test fish were returned to designated holding tanks for used fish. Throughout experiments, each fish was used only once.

Figure 3.2. Holding tanks at the ICER flume facility. 100L (A) and 3000L tanks (B).

3.5 Test species

3.5.1 Eurasian minnow

The Eurasian minnow, *Phoxinus phoxinus*, is a freshwater cyprinid species that occurs in fast-flowing streams and lakes in large parts of Europe and Asia (Fig. 3.3A). It is a potamodromous species (5-8 cm TL) which forms shoals throughout the duration of their life (max. 11 yrs). Eurasian minnows migrate mainly to shallow waters with gravel substrate for spawning (Kottelat and Freyhof, 2007). This migration takes place in early summer, when males change colour and their bodies become bulkier. Minnows are abundantly present in the UK, and are easy to keep in aquariums when sufficient oxygenised water and some form of current are present. Because of this, they have been the subject species in previous research involved with collective behaviour (Pitcher, 1973a, Partridge, 1980, Orpwood et al., 2008, Ward and Krause, 2001). Minnows were sourced from the Itchen River for use in experiments.

3.5.2 Chub

The chub, *Squalius cephalus*, is a grey, freshwater cyprinid species that occurs throughout large parts of Europe (Fig. 3.3B). They are considered a potamodromous species that inhabits slow-flowing habitats (e.g. lakes) as well as faster flowing streams and rivers (<50 $m^3 s^{-1}$), where cover is present (Bouchard et al., 1998, Kottelat and Freyhof, 2007). Chub are gregarious as juveniles (Kottelat and Freyhof, 2007), but solitary when adult, up to 22 years (up to 30 cm TL). Migration takes place over large distances to reach suitable spawning grounds characterised by shallow water depth and gravel substrate (Fredrich et al., 2003). Because of this, chub are susceptible to riverine barriers and should be considered in fish passage studies (Carter and Reader, 2000, Benitez et al., 2015). Juvenile 0+ year old chub were sourced from a fish farm in Calverton, UK for use in experiments.

3.5.3 Barbel

The barbel, *Barbus barbus*, is a brownish coloured, freshwater cyprinid species that occurs throughout Europe (Fig. 3.3C). It is considered a rheophilic species that occurs under a variety of habitats, included lakes and slow flowing rivers (Kottelat and Freyhof, 2007). They move from the banks of rivers to mid-channel habitats as they grow older and stronger and able to withstand fast flowing water >40 $m^3 s^{-1}$ (Britton and Pegg, 2011). The species is adapted for living on the bottom of rivers, having a flattened triangular body shape and strong pectoral fins. Barbules are located at the mouth, which help locate food on the riverbed. Adults can live well over 10 years and grow over 1 m TL. Both juveniles and adults tend to aggregate, especially in winter (EA, 2004, Kottelat and Freyhof, 2007). Barbel are important for European rivers as they are preferred by recreational anglers (Wheeler and Jordan, 1990), but are also an indicator species for river quality (Britton and Pegg, 2011). Barbel migrate considerable distances for spawning purposes (Baras and Cherry, 1990, Benitez et al., 2015), and longitudinal connectivity is deemed essential for maintaining healthy populations (Britton and Pegg, 2011). Since barbel can be delayed or blocked during upstream movements by small barriers (Lucas and Frear, 1997), or entrained on intake screens (Carter and Reader, 2000), it calls for suitable upstream and downstream passage facilities for this species. Juvenile (0+) barbel were collected from a fish farm in Calverton, UK, for use in experiments.

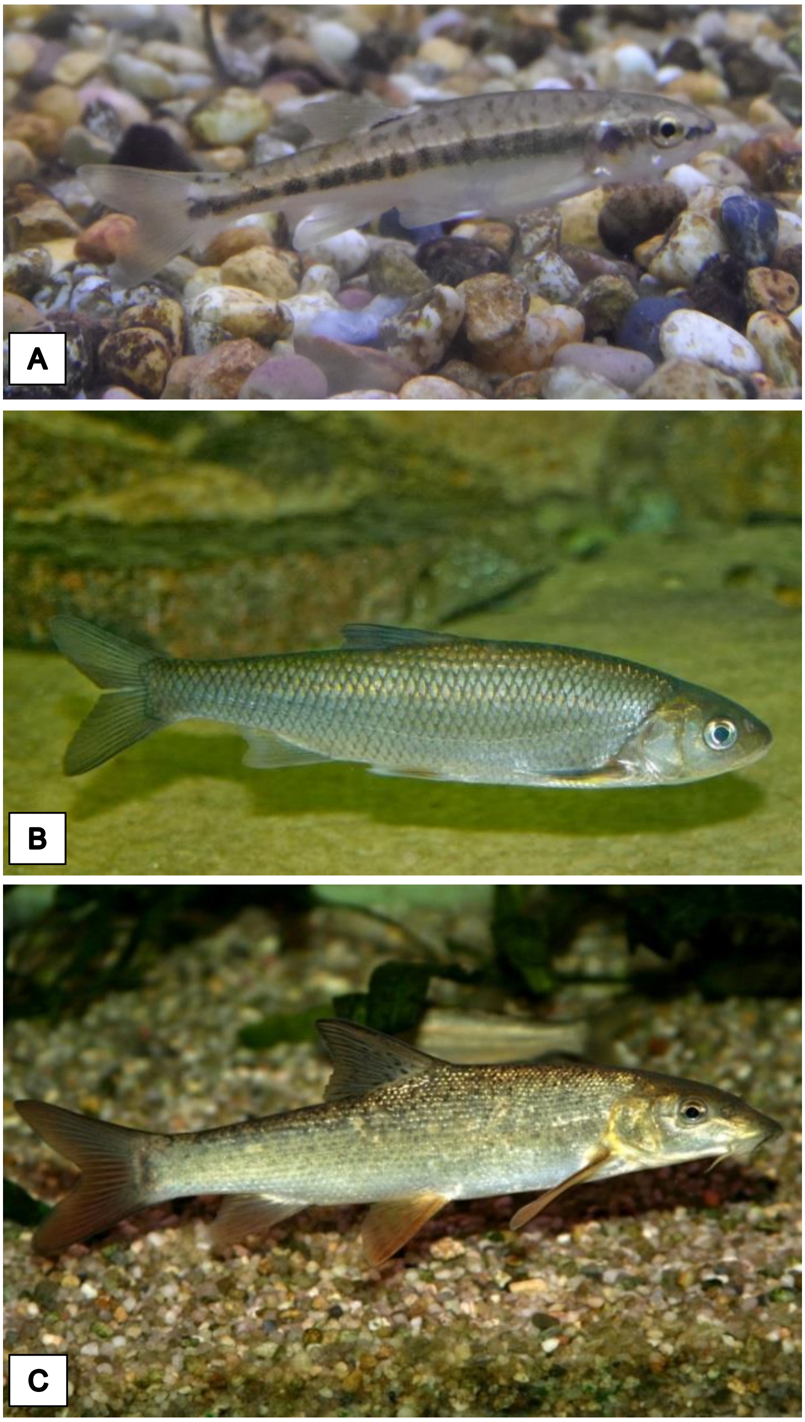

Figure 3.3. Species used throughout this research; Eurasian minnow (A), chub (B) and barbel (C).

Chapter 4: Collective fish behaviour in response to flow

Summary

It has long been suggested that individual fish benefit from occupying positions within groups by reducing energy expenditure, yet it is unknown whether this is a primary driver behind fish shoaling. This study addresses this question by means of flume experiments and Computational Fluid Dynamics (CFD) simulations. Pairs of Eurasian minnows (*Phoxinus phoxinus*) were tracked in a recirculating flume in the absence (control) and presence of flow (low and high) to test whether fish adopt an energetically more efficient shoal structure when costs are higher. Minnows spent more time shoaling under flowing conditions, and tended to swim in a tandem and side-by-side configuration under standing and moving water, respectively. Analysis of fish accelerations and velocity correlations indicated that the relative positions adopted in moving water reflected the individual's propensity to enhance information transfer with its neighbour. Simplified CFD simulations showed that the side-by-side configuration did not provide a hydrodynamic benefit in terms of drag experienced by the two fish. We conclude that optimising information transfer is a stronger driver for shoal formation than minimising energy expenditure, which, in turn, could be considered an effect rather than a cause of shoaling.

Keywords: *group behaviour, shoaling, schooling, energy saving, hydrodynamics, information transfer*

4.1 Introduction

Individual animals form and maintain groups when the associated benefits outweigh the costs (Alexander, 1974). Benefits of grouping include a lower risk from predators that results from enhanced chances of detecting or confusing them (Godin et al., 1988, Cresswell, 1994, Jeschke and Tollrian, 2007), increased foraging success (Creel and Creel, 1995, Day et al., 2001), and reduced energy expenditure during locomotion (Weimerskirch et al., 2001, Liao, 2007). Costs of group membership may include a higher detection and attack rate from predators, more competition for resources, and an increased probability of spreading disease (Lee, 1994, Krause and Ruxton, 2002).To profit from the presence of others, members of a group need to interact and transfer information effectively. The emergence of group patterns following such interactions is referred to as collective behaviour (Camazine et al., 2003, Couzin, 2009), and explains the ability of animal groups to maintain cohesion, synchronise movements, and respond to outside perturbations (e.g. a predator attack).

A variety of approaches are employed to better understand information transfer between individuals and the fundamental mechanisms underlying collective movement. Agent-based models can recreate group patterns observed in nature, based on the assumption that interactions between individuals are governed by simple rules of attraction, repulsion and alignment dictated by either topological or metric distance (Huth and Wissel, 1992, Couzin et al., 2002, Viscido et al., 2004, Hemelrijk and Kunz, 2005, Gautrais et al., 2008). Alternatively, interaction rules are inferred directly from observations over a range of group sizes for a variety of species, e.g. schools of 2 -300 golden shiner (*Notemigonus crysoleucas*) (Katz et al., 2011, Tunstrom et al., 2013), shoals of up to 8 mosquitofish (*Gambusia holbrooki*) (Herbert-Read et al., 2011), and flocks of hundreds or even several thousand of surf scoter (*Melanitta perspicillata*) (Lukeman et al., 2010) and European starling (*Sturnus vulgaris*) (Ballerini et al., 2008, Cavagna et al., 2010), respectively. While these studies suggest that our understanding of interactions between individuals is increasing, it remains far from complete.

The influence of physical factors, such as the characteristics of air or fluids that surround the group of animal under investigation, has not been systematically considered in previous work. Group structure is suggested to be strongly influenced by individual behaviours that attempt to minimize energy expenditure during locomotion (Fish, 1999). For example, great white pelican (*Pelecanus onocrotalus*) and bald ibis (*Geronticus emerita*) adopt an aerodynamically efficient flock structure when flying in V formation (Weimerskirch et al., 2001, Portugal et al., 2014). For fish, it has long been suggested that shoals should be arranged in a “diamond” formation that allows individuals to minimize drag and maximize thrust by exploiting vortices and wakes created by leading and neighbouring fish (Belyayev and Zuyev, 1969, Weihs, 1973). Research to verify theoretical predictions, however, has yielded contradictory results. The location of individual saithe (*Pollachius virens*), herring (*Clupea harengus*) and cod (*Gadus morhua*) within schools do not match the predicted patterns in terms of inter-individual distance (Partridge and Pitcher, 1979). Conversely, Atlantic bluefin tuna (*Thynnus thynnus*) adopt a school structure in which individuals may benefit hydrodynamically from nearest neighbours (Partridge et al., 1983). Research in this area is frequently based on experimental studies in which energy expenditure experienced by individuals within groups is assessed in swim chambers and quantified in terms of Tail Beat Frequency (TBF) and/or oxygen consumption. Under flowing conditions, the TBF of sea bass (*Dicentrarchus labrax*) and roach

(*Rutilus rutilus*) is lower for fish positioned at the rear of the group, compared to those at the front (Herskin and Steffensen, 1998, Svendsen et al., 2003). For sea bass, this is estimated to equal a 23% reduction in oxygen consumption, depending on swimming speed (Herskin and Steffensen, 1998). In groups of mullet (*Liza aurata*), individuals with low aerobic capacity usually trail others and thus exhibit a lower TBF to maintain position (Killen et al., 2011). In a recent study, every individual within a school of mullet exhibit a lower TBF than those swimming alone at the same speed (Marras et al., 2015). Thus, the evidence for the energetic benefits of being a member of flock, shoal or school has over time become increasingly convincing.

While experimental studies provide evidence that individual members can accrue energetic advantages by being part of a group, it remains unclear as to whether this is the primary driver behind group formation. If so, shoal structure would predominantly be hydrodynamically efficient and dictated by behavioural rules followed by individuals who seek to occupy energetically favourable positions. If not, shoal structure and individual positions are possibly governed by other factors, such as foraging and anti-predatory benefits (for an overview see Krause and Ruxton, 2002). For instance, it has been shown that in shoaling roach, individual positions vary with starved members occupying frontal positions to increase encounters with food (Krause, 1993b). Alternatively, by occupying frontal positions, fish are more likely to encounter predators (Bumann et al., 1997), and a centred position would be more beneficial for survival (Hamilton, 1971). Indeed, when exposed to an alarm substance, the positioning of a single minnow within a shoal of dace (*Leuciscus leuciscus*) changed so that it tended to be surrounded by other fish (Krause, 1993a). Finally, the structure of the shoal might come forth from an optimisation of information transfer by individuals (Camazine et al., 2003).

Using an experimental approach supported by Computational Fluid Dynamics (CFD) simulations, this study adopted a reductionist approach to investigate the response of a simplistic fish shoal, comprised of two individuals (Delcourt and Poncin, 2012), to the absence and presence of flow. Pairs of Eurasian minnow (*Phoxinus phoxinus*) were filmed in a section of a recirculating flume under either standing or flowing water. In this way the effect of flow velocity, and hence associated energetic costs, on shoal structure was isolated. By using automated tracking software to obtain the position and orientation of both individuals through time, we were able to investigate how: (i) shoaling time, (ii) shoal structure, and (iii) the nature of fish interaction was influenced by the presence and absence of flow. CFD simulations were also employed to test whether (iv) changes in shoal structure in response to the two flow treatments experienced were likely to bestow energetic benefits, in terms of drag.

4.2 Materials and Methodology

4.2.1 Experimental set-up

Experiments were conducted in a recirculating flume (12.0 m long, 0.3 m wide and 0.5 m deep) at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton. Two 5 mm mesh panels were inserted to create a 1.0 m long experimental area (Fig. 4.1). Two 85 W PhotoSEL Fluorescent lights were placed on wooden platforms above the flume to provide uniform illumination throughout the experimental area. The glass sides of the flume were covered on the outside in dark fabric to prevent external disturbance to the fish. Inside the flume, a layer of tape was attached to the glass sides to prevent fish from seeing their own reflection during trials. The discharge was monitored using a flow-meter and controlled with a valve installed on a recirculating pipe. A sharp crested weir was located at the downstream end of the flume to control the flow depth. An overhead camera was installed to record fish behaviour, and a white flume floor was used to enhance contrast between the fish and the background during video tracking.

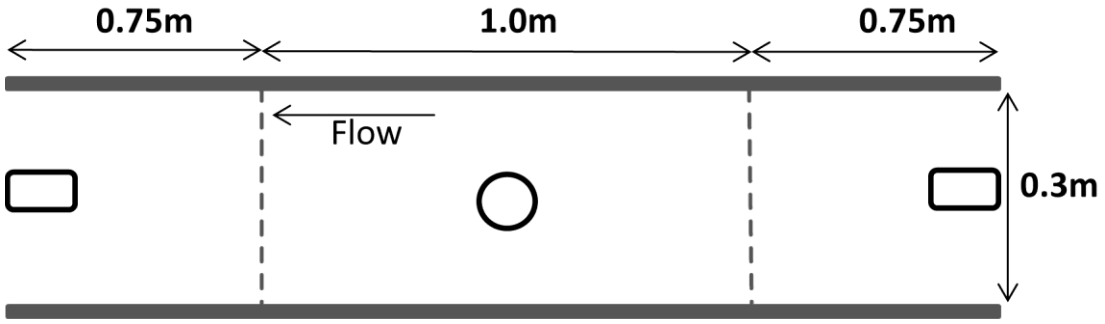

Figure 4.1. Plan view of the experimental setup in a recirculating flume at the ICER facility (University of Southampton). Thick grey lines represent the sides of the flume, with two mesh panels that bounded the domain (dashed lines); the circle represents the position of the overhead camera; rectangles represent locations of overhead light sources.

Experiments were conducted under standing water (control), and low and high velocity treatments under constant discharge of 0.001 $m^3\ s^{-1}$ (Table 4.1). Under these shallow water conditions, fish shoals were assumed to be two-dimensional. The magnitude of the high velocity treatment was determined through pilot experiments. At higher velocities, minnows were swept away by the flow and unable to prevent themselves from being impinged on the downstream mesh. Across two velocity treatments the Reynolds number of the flow (i.e. $Re = UH/\nu$) was kept constant by changing the water depth (Table 4.1). This was done in an attempt to maintain similar turbulence characteristics (turbulence intensity) across treatments and thus isolate the effect of flow velocity on fish and the structure of shoals. Other hydraulic characteristics (e.g. Turbulent Kinetic Energy, TKE) were possibly different between velocity treatments. However, considering the similar *Re*, these were deemed less important than the flow field, but are advised to be considered in further research (see Discussion).

Table 4.1. Hydraulic conditions encountered by Eurasian minnow pairs swimming in a recirculating flume under standing water and two flow treatments.

Treatment	**Water depth (cm)**	**Mean velocity (cm s^{-1})**	**Reynolds number (Re)**	**Froude number (Fr)**
Standing water	4.5	0	0	0
Low flow	6.0	5.74 ± 0.03	3021 ± 17	0.07 ± 0.0004
High flow	3.0	11.57 ± 0.08	3045 ± 21	0.21 ± 0.001

4.2.2 Experimental procedure

A total of two-hundred Eurasian minnows of mean body length (BL) ± S.E. = 52.6 ± 0.5 mm; mean wet mass (M) ± S.E. = 2.2 ± 0.1 g, were captured from the river Itchen (51°3’5.7” N, -1°18’59.1” W) using a seine net on 8 April 2013. They were transported in aerated river water to the ICER facility and maintained in a 500 L holding tank for two weeks. Four days before use in experimental trials, fish were transported to the hydraulics laboratory at the University of Southampton (a distance of approx. three miles) and placed into two 110 L holding tanks. Holding tanks contained dechlorinated and continuously oxygenated tap water. Water quality was maintained using submersible pond pumps, filter systems and water exchanges when necessary. Fish were fed flakes two times a day, at least two hours before being used in trials.

A total of 30 trials were conducted during May 2013, consisting of 10 replicas per treatment. Trials lasted 30 minutes and were conducted after 8pm to minimise the amount of scattered daylight present. Eurasian minnows were used as the species of consideration in this study. They are a member of the Cyprinidae family and are known to form shoals throughout their life, making them a suitable species for use in experimental research on collective behaviour (Pitcher, 1973b, Pitcher, 1973a, Partridge, 1982, Triantafyllou et al., 2004). For each trial, two Eurasian minnows were selected at random from the holding tanks (mean ± S.E. temperature = 20.2 ± 0.03 °C) positioned next to the upstream end of the flume.

Fish were transferred to the experimental area, with one of two lights switched on (alternated between trials). After five minutes the second light was switched on, and after a further five minutes of acclimation the trial commenced. After each trial, fish were collected, measured and weighed. Each fish was used once only, and treatments were alternated daily. Mean ± S.E. temperature of water in the flume at the start of a trial was 20.7 ± 0.16 °C. Pilot experiments revealed acclimation minimised startle response and erratic movements during trials.

4.2.3 Tracking and behavioural analysis

Video records of fish movements were analysed. Throughout trials, escape attempts through the mesh panels were commonly observed. During these attempts, fish were clearly interacting more with the mesh than with each other. Therefore, this ‘escape’ behaviour was excluded from analysis. Following the protocol of (Katz et al., 2011, Hensor et al., 2005), fish were deemed to shoal whenever they were within 4 BL distance of another fish. Using video data in which fish were actively shoaling, a five minute sample was selected and analysed for each trial. Activity along the lateral boundaries of the flume was minimal in standing water, but higher in flow treatments. Attempts were made to exclude video recordings of this activity unless insufficient sample time was available. Each video fragment was cut from original footage using VideoPad (v. 3.04), uncompressed using VirtualDub (v. 1.9.11) and loaded into a tracking software programme (Ctrax v. 0.3.9). A combination of threshold settings, applied to the contrast between the fish and background, determined the location and orientation of individuals through time (Fig. 4.2). The output of the tracking software was loaded into Matlab (R2012a). The ‘Fixerrors’ software toolbox allowed for frame-to-frame analysis of the tracking results, with a variety of possibilities to correct errors. Selected fragments was checked on a frame-to-frame basis before final export, which consisted of the *x*, *y* coordinates of every fish (i.e. their centre of mass) based on an arbitrary origin, as well as the orientation (radians) through consecutive frames. Coordinates were smoothed using a moving windows average of ten frames, as a final measure to eliminate minor tracking errors.

Shoaling time was expressed as a percentage of total time (adjusted for escape behaviour) spent shoaling during each trial. Mean shoaling time was calculated per treatment.

In consecutive frames of each video sample, the focal fish was placed at the centre of a Cartesian coordinate system (Fig. 4.3) and the relative position of the neighbour added to the corresponding bin. Total counts in all bins were combined for all video samples of the same treatment and expressed as a percentage of the most visited. Resulting density plots of *shoal structure* were produced in Matlab. Exported fish orientations in each sample were combined for all videos of the same treatment and rose diagrams produced.

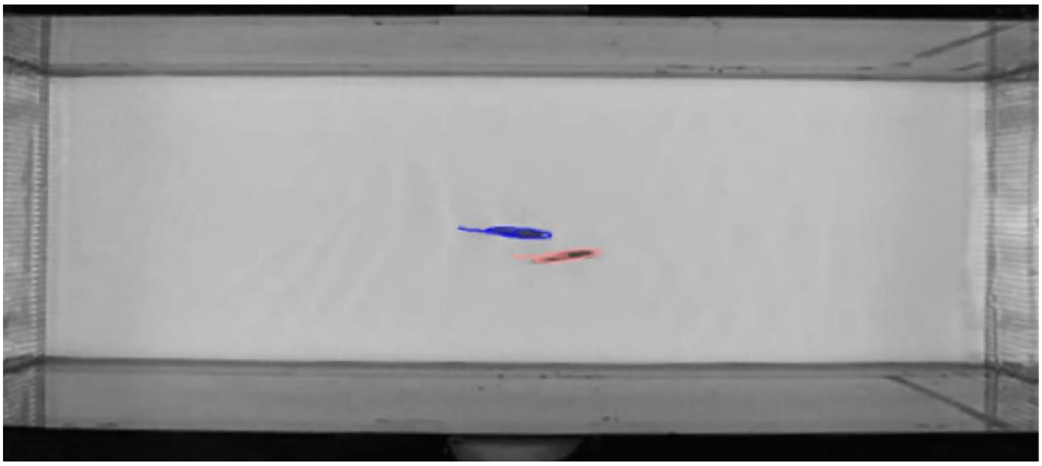

Figure 4.2. Snapshot image of a ‘High flow’ video selected for analysis. The experimental area is within the mesh panels on the left and right, and the two fish identified by the Ctrax tracking software.

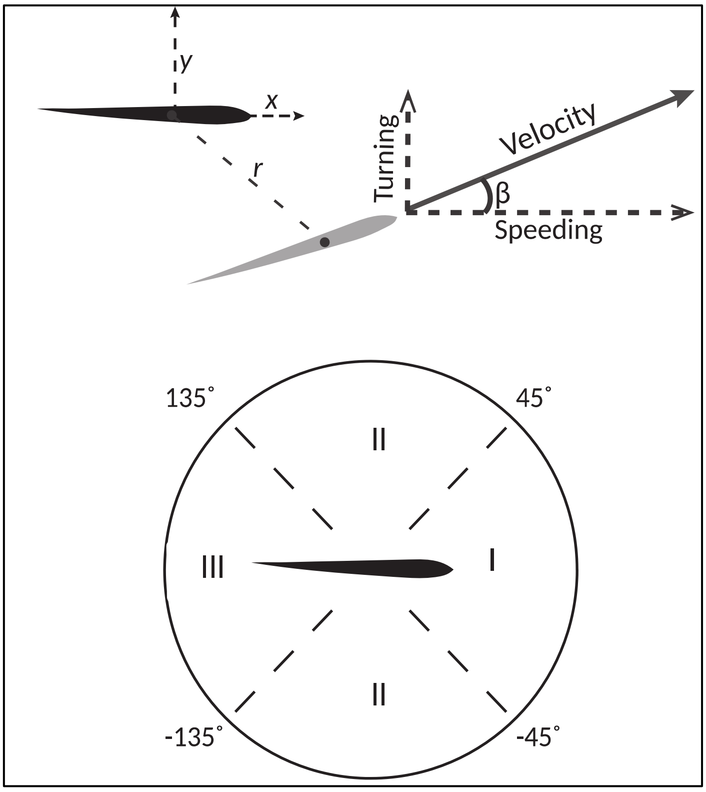

Figure 4.3. Focal fish coordinate system and division of its surrounding area into three regions. In consecutive frames, the focal fish (black) is placed at the origin of a fixed Cartesian coordinate system and the neighbouring fish (grey) at distance r away. Each fish has an orientation angle with the horizontal x-axis. Velocity can be decomposed into a speeding (along the x-axis) and turning (along the y-axis) component. The neighbouring fish can be placed into a specific region depending on its location with regards to the focal fish, defined as either in front of (I), to the side (II) or behind (III).

Interaction rules between individuals were quantified using fish velocities (ms^{-1}) and accelerations (ms^{-2}). These were calculated by numerical differentiation of the smoothed fish coordinates and velocities, respectively, in consecutive frames. Both speed and acceleration were decomposed in a ‘speeding’ (along the *x*- axis) and ‘turning’ (along the *y*- axis) component (Fig. 4.3). First, the response of the focal fish relative to the neighbour, in terms of speeding and turning acceleration, was calculated as a function of the distance between fish. Second, interactions between individuals and resulting information transfer can further be quantitatively expressed by means of correlation analysis (Cavagna et al., 2010, Katz et al., 2011). Here, velocity correlations functions were calculated as a function of time lag and of the relative position of the neighbour with respect to the focal fish:

$$C_s(dt) = \frac{\langle s_1(t)s_2(t+dt)\rangle - \langle s_1(t)\rangle\langle s_2(t+dt)\rangle}{\sqrt{\langle s_1(t)^2\rangle\langle s_2(t+dt)^2\rangle}}. \tag{1}$$

where *s1* is the speed of the focal fish and *s2* the speed of its neighbour. Angle brackets indicate ensemble averaging operators. The location of the neighbour was categorised as 4 equal sectors (Fig. 4.3): (i) in front of, (ii) to the side of, and (iii) behind the focal fish. For flow treatments, correlation analysis was restricted to frames where both fish were oriented against the flow. Drifting while oriented downstream was thus excluded, while holding station included.

4.2.4 Numerical analysis

A CFD approach was adopted to quantify the drag coefficient (C_d) of fish-type objects subjected to turbulent flow with bulk characteristics comparable to those under the ‘High flow’ treatment (Table 4.1). The mean (i.e. time-averaged) flow was resolved considering the simplest case of two solid individual fish, oriented in a side-by-side configuration. Assuming an incompressible fluid in adiabatic conditions, the mass and momentum balance equations governing the time-averaged flow are expressed by the Reynolds averaged Navier- Stokes (RANS) equations:

$$\frac{\partial \bar{u}_i}{\partial \bar{x}_i} = 0,$$

(2)

$$\rho \frac{\partial \bar{u}_j \bar{u}_i}{\partial x_j} = \rho \bar{f}_i + \frac{\partial}{\partial x_j}\left[-\bar{p}\delta_{ij} + 2\mu \bar{S}_{ij} - \rho \overline{u_i' u_j'}\right]. \quad (3)$$

where $u_i = \bar{u}_i + u_i'$, is the velocity component along the i^{th} direction; the overbar identifies the time-averaging component and the prime symbol identifies the fluctuating component; f is the body force vector, ρ is density, p is pressure, μ is dynamic viscosity, δ_{ij} is the Kronecker delta; and $\bar{S}_{ij} = \frac{1}{2}\left(\frac{\partial \bar{u}_i}{\partial x_j} + \frac{\partial \bar{u}_j}{\partial x_i}\right)$ is the mean strain rate tensor. Equations were closed using a Re-Normalisation Group (RNG) k-ϵ turbulence model and numerically integrated. Details on the free parameters and flow characteristics of the simulations are provided in Tables 4.2-4.3.

Table 4.2. Free model parameters and their values used in numerical simulations, where the RNG k-ϵ turbulence model was employed to model the drag on two side-by-side fish under the 'High flow' regime from experimental work.

Symbol	Interpretation	Units	Value
$C_{1\epsilon}$	RNG constant of dissipation	-	1.42
$C_{2\epsilon}$	RNG constant of dissipation	-	1.68
C_{μ}	RNG constant of viscosity	-	0.0845
β	RNG constant of turbulence	-	0.012
η_o	Starting ratio turbulent to mean time scale	-	4.38

Table 4.3. Flow characteristics and their values used in numerical simulations.

Symbol	**Interpretation**	**Units**	**Value**
σ_k	Prandl number for turbulence	-	0.7194
σ_ϵ	Prandl number for dissipation	-	0.7194
ρ	Density	kgm^{-3}	998.2
T	Temperature	K	288.16
μ	Dynamic viscosity	$kgm^{-1}s^{-1}$	0.001
v_{inlet}	Inlet flow velocity	ms^{-1}	0.1157
I	Turbulence intensity	%	2.0
d	Hydraulic diameter	m	0.006
Re_{foil}	Reynolds number of foil ($v_{inlet}d\rho/\mu$)	-	700

The domain and fish proxies being used throughout simulations were created with Computer-Aided Design (CAD) software and scaled to be approximately the same as those used in the experimental procedure. The size of the computational domain was 20x11x10 BL. Fishes were placed 5 BL from the upstream and side boundaries. To represent fish, a NACA0015 (*xy*- plane) with a NACA0009 (*xz*- plane) air foil geometry were used which proved to represent the three-dimensional shape of the minnows very well. Fins and other details of the fish were not reproduced. The fish and domain geometry were divided into a mesh of tetrahedral cells. The computational mesh contained approximately 550k cells with regions of increased cell density near the foils, in particular near the head and tail sections (Fig. 4.4). With this configuration, the results from the simulations showed to be independent of mesh-size and convergence was reached well.

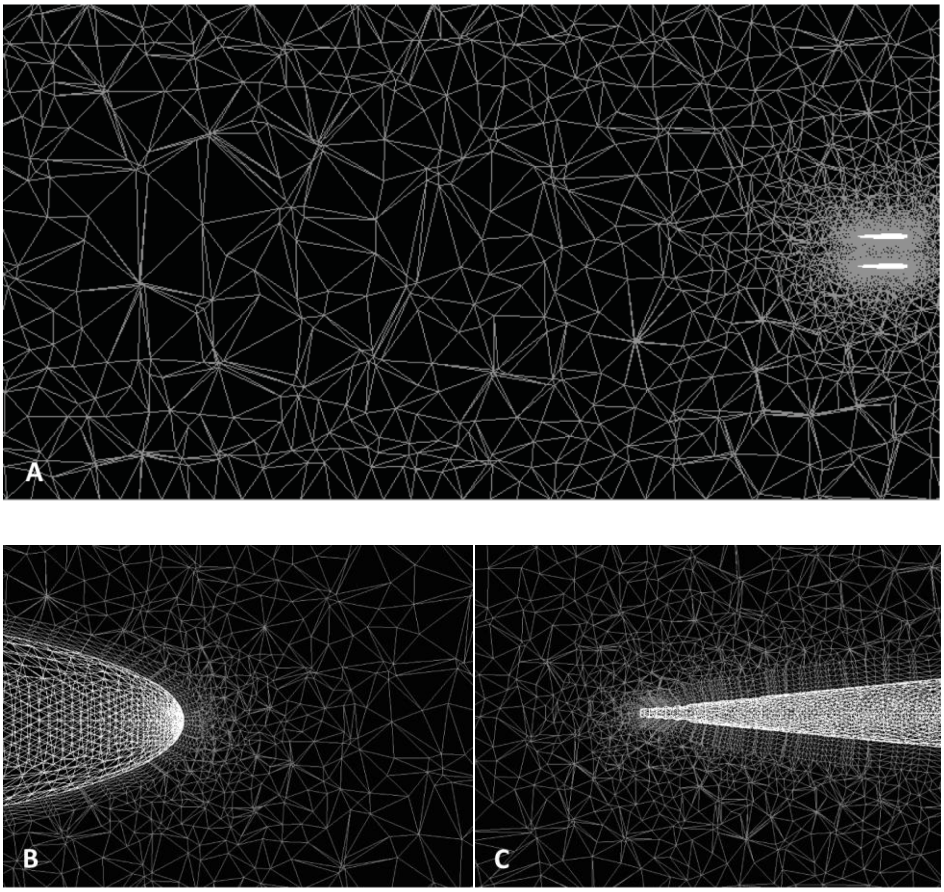

Figure 4.4. XY -projection of the computational mesh applied to 3-D simulations. (A) total domain; (B) mesh in proximity of the head; (C) mesh in proximity of the tail. The adaptive mesh used in simulations included characteristic cell size of a maximum of 0.07 m away from the fish and $1.66 \cdot 10^{-4}$ m in proximity of fish surfaces.

At the upstream part (inlet) of the domain, boundary conditions were set to specific values for free flow velocity (v_{inlet}), derived from experimental work. The outflow boundary conditions (downstream part of the domain) were set to enforce continuity (mass conservation) throughout. Symmetry boundary conditions were set for the lateral boundaries of the domain, meaning all the fluxes of relevant quantities (e.g. mass, momentum) were forced to zero. At the simulated fish boundaries, the no-slip condition was applied combined with a wall function to solve the flow in the immediate proximity of the fish surfaces. We performed an extensive sensitivity analysis and results on the drag coefficient were weakly dependent on dissipation and TKE levels imposed at the domain boundaries. In particular trends of the drag coefficient were essentially independent. Values for turbulent kinetic energy (*k*) and dissipation (ϵ) at the boundaries were estimated using parameters listed in Table 4.2-4.3:

$$k = \frac{3}{2}(v_{inlet}I)^2, \tag{3}$$

$$\epsilon = C_\mu^{\frac{3}{4}} \frac{k^{\frac{3}{2}}}{0.07d}. \tag{4}$$

For spatial discretisation, second order upwind schemes were used to calculate variable values at cell boundaries. In all computations, solutions were considered correct (‘converged’), if changes were within a tolerance value of 10^{-5}. As a proxy for energy expenditure, the drag coefficient of individual fish in a side-by-side configuration ($C_{d,side}$) was then computed for different lateral distances as $C_{d,side} = \frac{2F_d}{\rho A U^2}$, where F_d is the drag force derived from the simulations, A is the frontal area of individual fish and U^2 is the upstream undisturbed mean velocity. Drag coefficients of a single, solitary fish ($C_{d,solitary}$) were also calculated. The normalised drag coefficient of each fish in a side-by-side configuration was then computed as $C_d^* = \frac{C_{d,side}}{C_{d,solitary}}$ and plotted as function of the distance between them, normalised by their body length (BL), denoted by d^*.

4.2.5 Statistics

Percentage data were arcsine square root transformed before tests of normality and homogeneity of variance were performed using a Shapiro-Wilk and Levene’s test, respectively. A one-way ANOVA was used to assess the influence of treatment (fixed) on shoaling percentage (dependent variable), followed by a Tukey HSD post-hoc test to identify which treatments were significantly different.

4.3 Results

Shoaling time: Minnows tended to shoal more in flowing than standing water (Fig. 4.5). Shoaling time differed between treatments ($F_{2,27}$ = 4.523, P = 0.020) and under high flow was significantly higher than in standing water (P = 0.017).

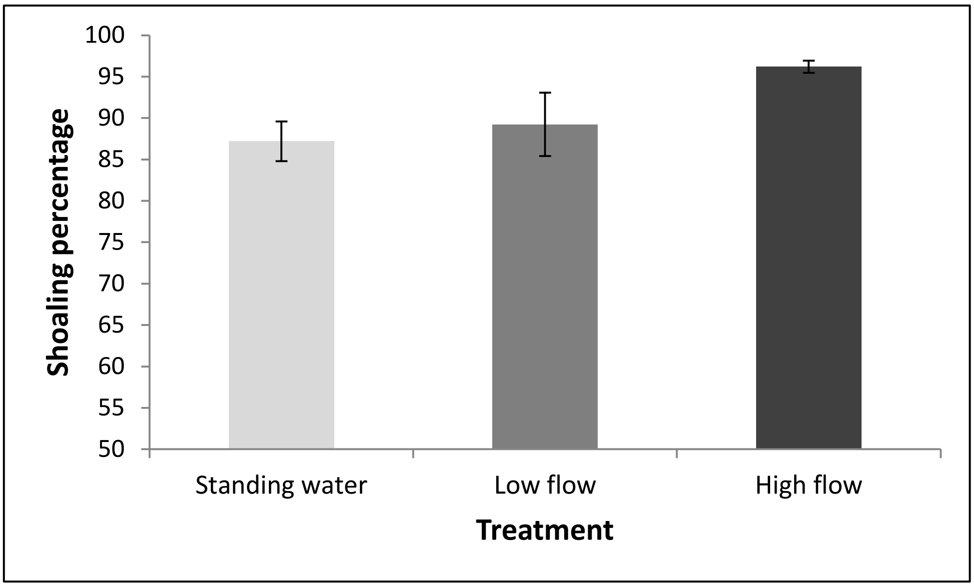

Figure 4.5. Shoaling time of Eurasian minnow pairs. This is expressed as the percentage of total time fish spent shoaling, which was adjusted for escape behaviour at the mesh panels.

Shoal structure: In standing water, the distribution of the neighbour relative to the focal fish formed an ellipse with major and minor axis up to 1.0 and 0.5 BL, respectively. The neighbour tended to be present more often in regions immediately in front or behind the focal fish, thus the pair resembled a tandem configuration while swimming (Fig. 4.6A). Fish predominantly oriented themselves along the 0° and 180° direction relative to the *x*-axis (Fig. 4.6B). Under low flow, the neighbour showed a more uniform distribution around the focal fish of distances up to 1 BL, comparable on the *x*- axis to those observed for the standing water condition (Fig. 4.6C). Conversely, under high flow the neighbour tended to occupy positions along the sides of the focal fish, to a maximum of approximately 0.5 BL away (Fig. 4.6E). Under both flow treatments, fish tended to adopt more polarised orientations (between -20° and 20°) compared with the control, facing the direction of flow, while active downstream movement was rare (Fig. 4.6D,F).

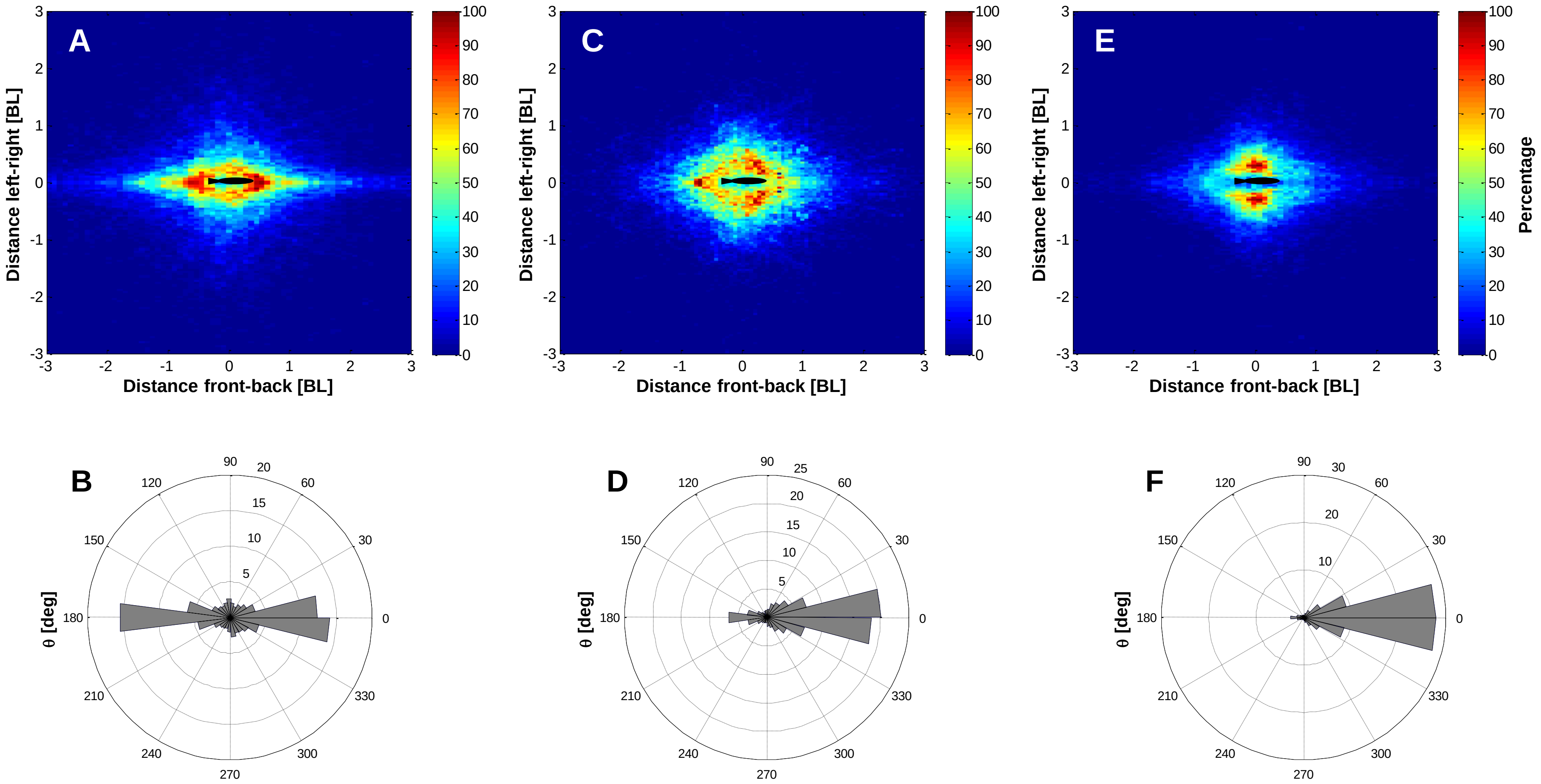

Figure 4.6. Contour density plots and orientation histograms of shoaling Eurasian minnow pairs. The position of the neighbouring fish with respect to the focal fish (top) and the frequency of orientations of both fish (bottom) are shown for standing water (A-B), low flow (C-D) and high flow (E-F). For the density plots, the domain plotted is [-3 BL, 3 BL], where BL is the average body length of fish used in the associated treatment. The black fish shape denotes the location of the focal fish in the origin. Length of each angle histogram is a measure of the frequency (percentage) with which Eurasian minnows are oriented in a particular direction. In graphs C-F, flow is from right to left.

Interaction rules: Under all treatments, the focal fish exhibited deceleration when the neighbour was behind, and acceleration when in front (Fig. 4.7A, C, E). The turning component of the focal fish's acceleration decreased as the neighbour moved farther to the left (indicating a turn to the left), and increased when the neighbour was located farther to the right, indicated by a positive acceleration (Fig. 4.7B, D, F). Analysis of temporal correlations of both components of each fish's velocity showed that, in standing water, these were highest when the neighbour swam in front, i.e. the focal fish responded best when swimming behind it (Fig. 4.8A,B). This is in agreement with the tandem configuration predominantly observed under this treatment.

Peaks in the velocity correlation functions are then associated with a time scale that can be interpreted as the response time of the focal fish to movements of the neighbouring fish, and were typically between 0.3 and 0.5s. The occurrence of peaks in all correlation curves except those for when the neighbour was located behind the focal fish indicated that information transfer did not flow from back to front. Under standing water this means that the front fish is leading, and not responding to changes from the trailing fish. In turn, this fish can employ its senses (vision and lateral line) to see and detect the front fish's movements and respond accordingly (at ~ 0.5s).

Under flow treatments, both the speeding and turning velocity correlation functions showed strikingly different features. First, a general increase in correlation values for the speeding velocity component indicated that fish, besides aiming to shoal more (Fig. 4.5), interacted in a more coordinated way in moving water (Fig. 4.8C,E). Second, highest correlations for the turning component of the velocity were found in the side-by-side configuration (Fig. 4.8D, F). Finally, regardless of which individual was chosen as the focal fish or neighbour, the correlation functions always displayed a maximum, indicating that the exchange of information between the two was mutual and no longer in one direction as observed for the tandem configuration. The combined observations suggest that when a flow field is present, staying behind the front fish is not desirable, as responding to its movements (especially turning) cannot longer be optimally detected through the functioning of the lateral line. Through a side-by-side configuration, visual contact is thus enhanced which allows for more optimal coordinated movements, in particular when changing direction.

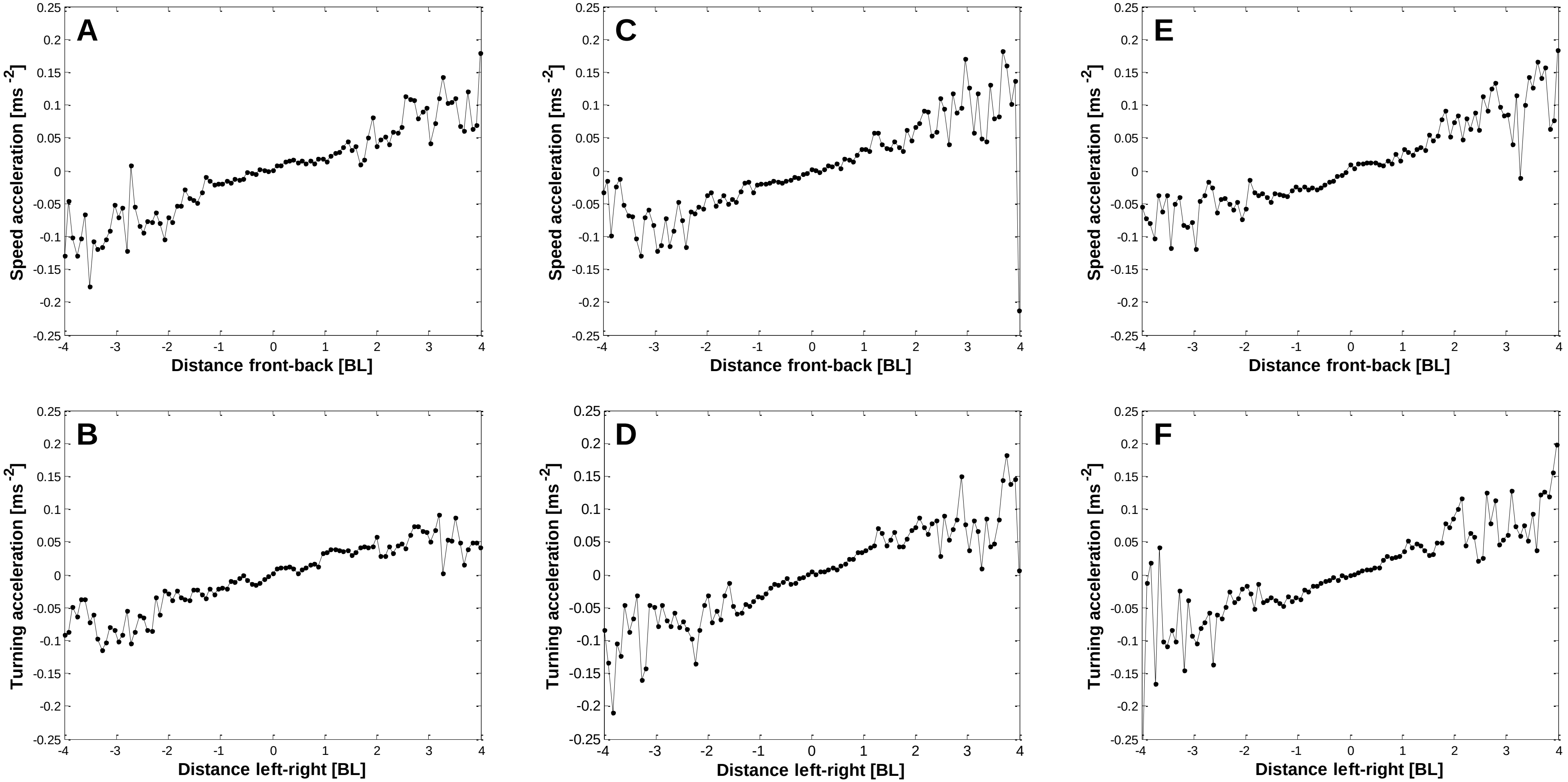

Figure 4.7. Mean accelerations of the focal fish vs. the distance of the neighbouring fish. The speeding and turning component of the acceleration is shown in the top and bottom panel, respectively, for standing water (A-B), low flow (C-D) and high flow (E-F). For the speeding components, positive (negative) distances indicate a neighbouring fish in front of (behind) the focal fish. For the turning components, positive (negative) distances indicate a neighbouring fish to the left (right) of the focal fish.

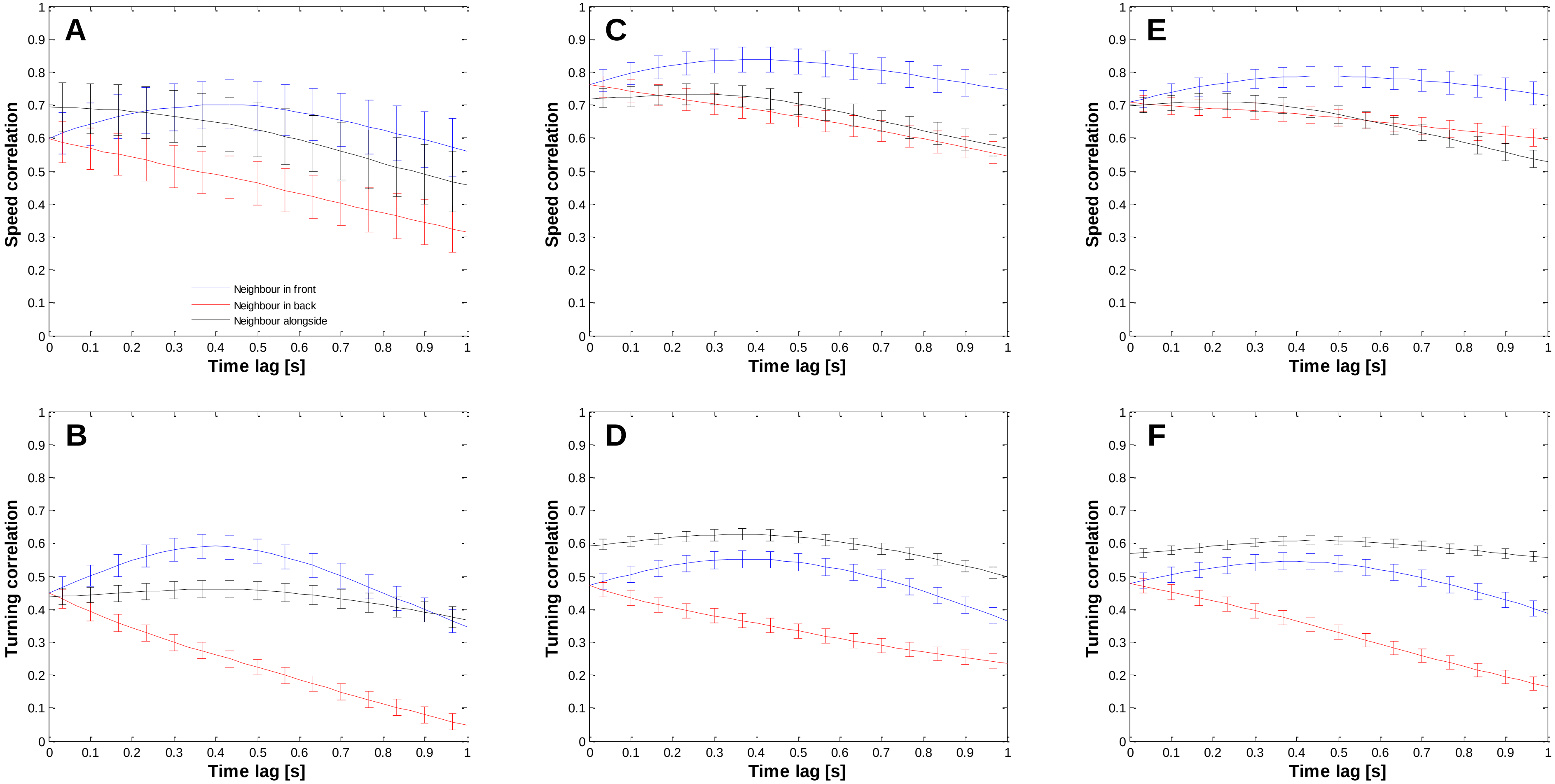

Figure 4.8. Temporal velocity correlations depending on relative position of neighbouring fish. Mean correlations (with 95% confidence intervals) of the focal fish at time t+dt with respect to the neighbouring fish at time t, when it is either in front (blue), behind (red) or to the side (black). The speeding and turning component of the velocity is shown in the top and bottom graph, respectively, for standing water (A-B), low flow (C-D) and high flow (E-F).

Numerical analysis: The drag coefficient (C_d^*) of both fish was inversely related to the distance (d^*) between them (Fig. 4.9) until it approached a plateau corresponding to the case of an isolated individual. As fish generally experience more viscous than pressure drag forces due to their streamlined shape (Vogel, 1994), it follows that the higher the velocity around the fish, the higher the drag forces exerted by the fluid. Indeed, the mean velocity of the fluid was negatively correlated to the distance between the fish (Fig. 4.10).

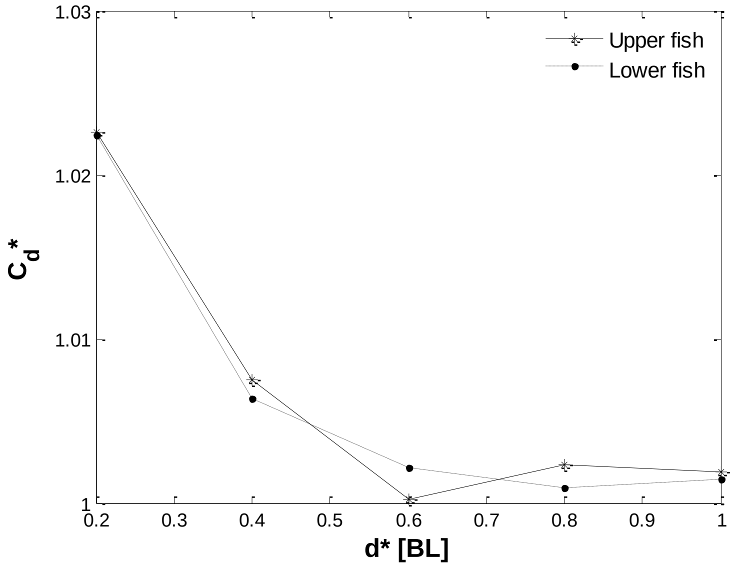

Figure 4.9. Drag coefficient, normalised by that of a solitary individual, (C_d^*), on two side-by-side oriented fish as function of normalised (by BL) lateral distance between them (d^*). The solid (dotted) line represents the drag coefficient of the upper (lower) fish, following the simulation setup as shown in Fig. 4.4A.

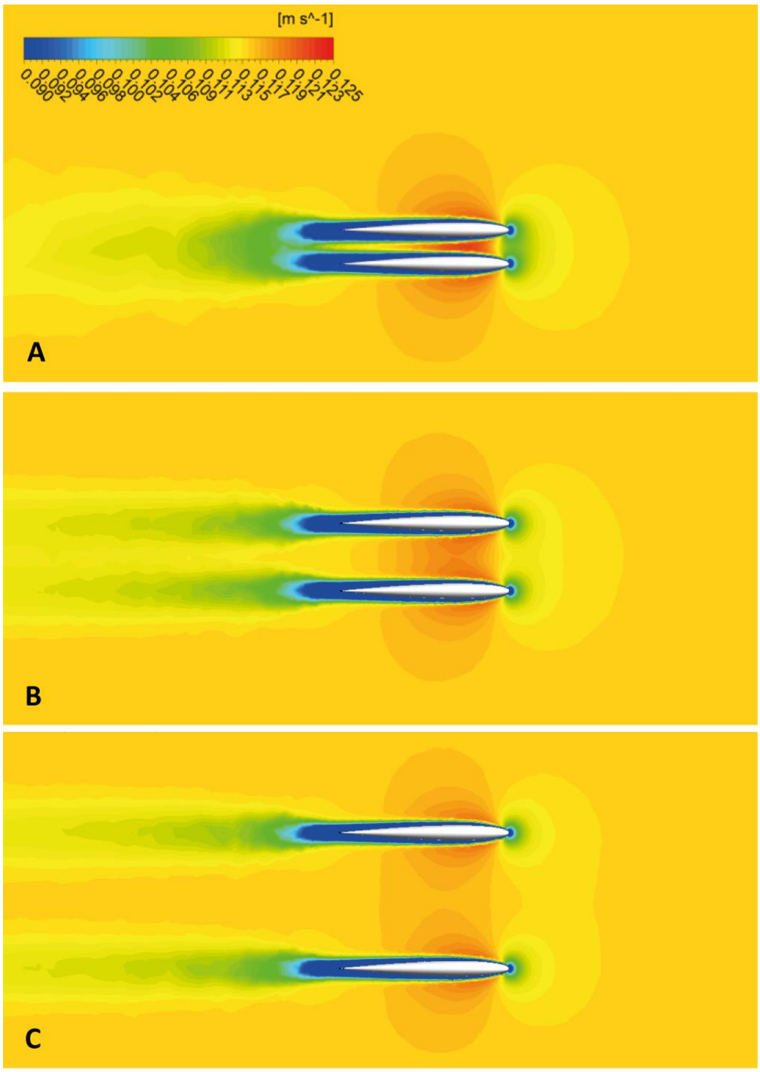

Figure 4.10. Mean velocity contour plot around two side-by-side oriented fish, being projected onto a xy-plane going through the fish. Results are shown for the cases d*= 0.2 (A), 0.4 (B), and 0.8 (C).

4.4 Discussion

This study investigated the collective behaviour of minnows in the absence and presence of flow. Our results indicated that optimisation of information transfer between individuals is likely a stronger driving force behind group formation in this species, rather than energy saving through adoption of a hydrodynamically efficient configuration. Our findings contradict the current long-standing hypothesis the group structure of shoaling fish have evolved primarily as a means to minimise energetic costs (Krause and Ruxton, 2002, Fish, 1999).

Pairs of minnows were used in this study, as this is the smallest possible social unit, and thus eliminates the effect of multiple sources of social information to an individual (Delcourt and Poncin, 2012). A similar approach has been used in the past, both for experimental work with hydrofoils or flapping foils (e.g. Dong and Lu, 2007, Boschitsch et al., 2014, Dewey et al., 2014, Becker et al., 2015) and with live fish (e.g. Herbert-Read et al., 2011, Katz et al., 2011, Ashraf et al., 2016). Results with pairs of foils provided valuable information on wake characteristics and movement patterns, but it has been recognized that larger shoals are more complex which should be addressed in future work (Dewey et al., 2014). Using live fish, Herbert-Read et al. (2011) analysed interactions in mosquitofish pairs and then increased shoal size to 4 and 8 individuals; Katz et al. (2011) investigated golden shiner pairs followed by groups of, 3, 10 and 30 fish; and Ashraf et al. (2016) studied red nose tetra fish (*Hemigrammus bleheri*) in two and three fish shoals. Importantly, in all cases the results showed that pairwise interactions persisted in bigger shoals. Furthermore, in the larger golden shiner and mosquitofish shoals, interactions with the nearest neighbour became more important as shoal size increased, although the magnitude of interactions, in terms of speed regulation, decreased (Katz et al., 2011, Herbert-Read et al., 2011). This could indeed be a consequence of the increased complexity of information transfer with a single neighbour when many are present. Ashraf et al. (2016) report that interactions in three fish shoals are similar to those found in pairs, in terms of distance between focal fish and nearest neighbour and synchronisation of swimming motions. How that changes in more complex shoals is part of their ongoing research. Even though minnow shoals in nature usually consist of many individuals (Kottelat and Freyhof, 2007), the importance of a single nearest neighbour could thus very well be applicable to larger shoals. Video footage of three-fish shoals has been collected and the analysis will be part of future research.

Across treatments, Eurasian minnows tended to display shoaling behaviour, which became significantly more frequent under higher flows. There are multiple explanations for this, including an anti-predator response to reduced swimming manoeuvrability (Liao, 2007), or to take advantage of an opportunity, as there are costs associated with locomotion and currents carry particles of food for which shoaling provides an efficient vehicle of detection (Day et al., 2001, Krause, 1993b, Pitcher et al., 1982).

Shoal structure was different between standing water and high flow. In standing water, fish tended to stay in close proximity to each other, as their positions resembled a tandem configuration. Conversely, under flowing conditions, fish predominantly adopted positions alongside each other. Our findings support (Chicoli et al., 2014) who observed groups of eight giant danio (*Devario aeguipinnatus*) adopt a side-by-side configuration in moving water. The authors suggest that under standing water individuals use both the lateral line and vision to sense the presence of neighbours with whom they exchange information. Under flowing water conditions this is not the case because the mechanosensory cues detected by the lateral line may to some extent be masked. Therefore, they speculate that the side-by-side configuration, in which visual contact is maintained, compensates for the lack of reliable information obtained using the lateral line. Interestingly, under standing water, fish with disabled lateral lines tend to associate more with neighbours oriented alongside, compared to control and blinded fish, indicating that fish enhance opportunities for visual contact when lateral line functioning is diminished (Partridge and Pitcher, 1980).

Our explanation for the occurrence of the side-by-side configuration deviates from that previously proposed (Chicoli et al., 2014). Regardless of whether the water was quiescent or moving, shoal cohesion and structure was largely similar to that predicted using interaction rules commonly adopted in agent-based models. Fish are attracted to each other at greater distance and maintain a certain distance between each other at close range (e.g. Couzin et al., 2002). This is accomplished by means of acceleration/ deceleration, and resembles findings on golden shiners (*Notemigonus crysoleucas*) (Katz et al., 2011). We suggest that in this study shoal structure was a result of the behaviours enacted by both fish, rather than due to unilateral actions of one in response to the other. However, we observed no clear zones of repulsion close to an individual, as previously reported for similar shaped fish (Katz et al., 2011, Herbert-Read et al., 2011). Instead, minnows accepted occasional contact with each other while changing position and this might be a species specific characteristic. These observations allow us to hypothesize that the adoption of a side-by-side configuration is not a result of a collision avoidance strategy, but might indeed aid in improving visual contact and ultimately collective movement. This was investigated through analysis of velocity correlation functions.

Peak response times were found to be around 0.5s, matching speed correlations as reported for golden shiners (Katz et al., 2011). The velocity correlation functions further indicated that information transfer in the forward direction did not occur between fish under the experimental conditions described, regardless of whether water was flowing or not. This suggests that, under standing water, minnows did not utilise mechanosensory cues to communicate in the forward direction when one fish was positioned in the blind spot of the other, as suggested possible by (Chicoli et al., 2014). Instead, the front fish chose a certain path and the trailing fish followed. Under flowing water, where front-to-back information transfer might be masked by the properties of the flow, the adoption of the side-by-side configuration enhanced mutual information transfer, especially for turning motions, through promoting visual contact, a possibility also suggested by (Chicoli et al., 2014).

Our CFD simulations were performed with static foils rather than moving fish. Therefore, they do not fully represent the complex interactions between moving fish and conspecifics or the surrounding flow in terms of energy expenditure. For instance, these simulations do not allow us to discount potential benefits of a side-by-side configuration in terms of any thrust generation, as the fish were not modelled to move their body and fins were not reproduced. Thrust represents a substantial energetic cost for swimming fish, and interactions between fins have been shown to can significantly influence thrust efficiency, as shown by Drucker and Lauder (1999) and Akhtar et al. (2007) for dorsal-tail and caudal-tail fin motions in bluegill sunfish (*Lepomis macrochirus*). Conversely, the simulations and the experiments carried out by Dong and Lu (2007), Dewey et al. (2014), and Hemelrijk et al. (2014) indicate that thrust generation on side-by-side swimming fish is unlikely to be higher than that of a single fish at distances observed here. Using our simplified approach, results show that fish in a side-by-side configuration do not benefit from a reduction of drag for the distances observed. However, more detailed simulations with moving minnow shaped fish would be required to provide better information on the energetic consequences when swimming alongside each other.

4.5 Conclusions

The presence of flow is unambiguous in riverine systems, and brings along energetic costs to fish, whether living solitary or in shoals. Results of this study have shown that for shoaling minnow pairs the presence of a flow field (and thus higher energetic costs) significantly promoted the time spent shoaling compared to standing water. A notable difference in shoal structure was furthermore present, as a tandem configuration under standing water changed to a side-by-side configuration under (high) flow. In this configuration, both fish achieved highest turning velocity correlations; possibly by improving visual contact as lateral line functioning is affected by the properties of the flow. Simplified CFD simulations further seemed to indicate that neither fish was saving energy through reducing drag.

This study provides an important step forward in understanding social interactions between shoaling fish. Further work is needed to identify the flow characteristics (e.g. flow velocity, Reynolds number, Turbulent Kinetic Energy) that cause fish to adopt alternative group structures. Furthermore, other factors that influence their behavioural response (such as a requirement for food in a costly environment, or a predatory threat) cannot be fully excluded and should be investigated. Such information could help quantify how anthropogenic alteration of river hydrodynamics, e.g. as a result of the construction of dams and weirs, may affect social interactions in moving groups of fish, an important factor in collective migration and its evolution (Guttal and Couzin, 2010). Finally, it is important to extend this research to consider larger fish groups to investigate how individual fish integrate information obtained from multiple social sources under flowing water conditions.

Acknowledgments

The numerical analysis was performed by Riccardo Callegarin (Università degli Studi di Padova, Italy) as part of his MSc thesis. Special thanks to him for the assistance in this study.

Chapter 5: Effectiveness of horizontally and vertically oriented bar racks to guide juvenile chub (*Squalius cephalus*) and barbel (*Barbus barbus*) under experimental conditions

Summary

Physical fish screens are designed to prevent entrainment of fish into intakes, and divert them to a safe alternative route, such as a bypass channel. Bar/trash racks are commonly used, but their functioning has predominantly been assessed for diadromous species. This study compared the efficacy of horizontal and vertical bar racks for guiding downstream moving groups of five chub (*Squalius cephalus*) and barbel (*Barbus barbus*) in a recirculating flume under two discharge regimes. Hydrodynamics results showed that regardless of rack type or discharge, the mean flow was directed through the racks and sweeping flows towards the bypass changed little in magnitude. The racks had limited success in diverting either species, with 39.9% (chub) and 29.7% (barbel) of fish released entering the bypass channel. Entrainment through the racks was similar with 39.7% and 22.4% for chub and barbel, respectively. Guidance efficiency (number of times a fish entered the bypass as percentage of total approaches) were comparable between species low (mean of 21.3% and 24.8% for chub and barbel, respectively. Differences between the horizontal and vertical orientation were inconsistent, although the number of fish that was guided along the rack was higher for vertical ones. Interspecific differences were found for the number of entrained/ diverted fish, and avoidance responses, all of which were higher for chub than barbel. Shoal cohesion was variable and more pronounced in chub. Both species behaved more as shoals than individuals under low discharge.

From this study, it is concluded the used bar racks are not suitable for guiding juvenile cyprinids under the tested conditions. Incorporating interspecific differences in avoidance behaviour are a key in developing multi-species screening solutions, such as bar racks.

Keywords: Fish screens, bar racks, guidance efficiency, Cyprinidae, groups.

5.1 Introduction

Freshwater ecosystems continue to be affected by mankind through activities associated with power generation, water supply and irrigation, which require implementation of riverine infrastructure (Malmqvist and Rundle, 2002). Large river systems, which account for 60% of the world’s annual runoff, are fragmented by large dams (> 15m high) (Nilsson et al., 2005), and numerous smaller-scale barriers are further present in rivers (Kemp and O'Hanley, 2010). The effect of such impoundments ranges from alteration of hydrological and geomorphological properties of the river (Graf, 2006), to changes in water chemistry (Humborg et al., 1997), to changes in biodiversity through habitat loss (Fahrig, 2003, Vörösmarty et al., 2010). Fish are particularly susceptible to the presence of barriers, as connectivity between habitats that are essential to their lifecycle is reduced (Lucas and Baras, 2001). Fish migration can be impeded or completely blocked (Lucas and Frear, 1997, Russon et al., 2011), while downstream migrants run the additional risk of getting entrained at intakes which can lead to mortality or injury (Schilt, 2007).

Efforts to mitigate the impact of impoundments for fish include technologies that aim to protect migrants and facilitate passage (Clay, 1995). For example, fishways are structures that incorporate flow-reducing elements in a series of steps, allowing the ascent of upstream migrating fish (Bunt et al., 2012). From a historic perspective, upstream passage has received much attention, while the importance of protecting returning fish was recognised later on (Katopodis and Williams, 2012). Techniques to protect downstream migrants include behavioural barriers that deter fish away, or physical screens that prevent entrainment and guide fish to a safe bypass channel (Larinier and Travade, 2002). Currently, there are various acts of legislation in place that oblige the provision of fish passage facilities or screens at dams or offtakes (for an overview, see Kemp, 2016). However, evaluation of these has traditionally been biased towards diadromous species while the wider community (e.g. cyprinids) has largely been ignored (Noonan et al., 2012, Williams et al., 2012).

A commonly used type of physical screen is the bar rack, which closely resembles trash diverters that are often in place to prevent debris from entering turbines (Katopodis and Williams, 2012). Evaluation of the guidance efficiency of bar racks has yielded variable, sometimes low values: between 40% and 98% for American and European eels (*Anguilla anguilla* and *A. rostrata)* (Amaral et al., 2003, Russon et al., 2010, Gosset et al., 2005, Calles et al., 2012), between 17% and 73.3% for Atlantic salmon (*Salmo salar*) smolts (Scruton et al., 2003, Croze, 2008, Calles et al., 2012), and between 0% and 52% for brown trout (*Salmo trutta*) smolts (Greenberg et al., 2012). Reported efficiencies of bar racks for other species can also be under 50% (EPRI, 2001). To improve the performance of bar racks for multiple species, a better understanding is required on the factors that limit their efficiency.

The effectiveness of physical screens is found to be dependent on interspecific differences between the species and life stages under consideration, as well as local hydrodynamic conditions. For example, salmonid smolts tend to be surface oriented during downstream movements (Coutant and Whitney, 2000), whereas eels prefer to stay at the bottom (Russon et al., 2010). When the flow velocity close to the screen cannot be overcome by the fish, they risk being entrained/ impinged or injured during prolonged contact with screen elements (White et al., 2007, Poletto et al., 2014). An avoidance response to hydrodynamic conditions encountered at the bypass entrance has also been observed for downstream migrants (e.g. Ovidio et al., 2016). To promote guidance, current design criteria state screens should be angled towards the oncoming flow, with a bypass located at the downstream end (EA, 2009). Such placement of the screen induces a local sweeping velocity (parallel to the screen) to enhance guidance, while an escape velocity (perpendicular to the screen) prevents entrainment/ impingement when sufficiently low. The magnitude of both velocity components depends on the screen angle, and factors such as bar spacing and shape (Katopodis et al., 2005, Rajaratnam et al., 2010). Depending on the target fish species and life stage, different thresholds for the escape velocity are prescribed (Turnpenny et al., 1998, EA, 2009). Finally, the role of fish’s behavioural response to the hydrodynamic conditions encountered at screens is deemed essential and a key to successful guidance (Williams et al., 2012).

A recent development in use of trash or bar racks, is aligning bars horizontally, instead of vertically, mainly for the purpose of facilitating self-cleaning, but it has also shown promise to guide fish (Ebel, 2008, Ebel et al., 2015). Given the oval body shape of most fish, it is hypothesised that blocking will occur sooner with horizontally compared to vertically aligned bars. Conversely, a fish can be blocked with a higher bar spacing when this horizontally aligned, allowing for more water abstraction. Furthermore, entrainment through horizontal bars is presumably less disturbing to fish as their pectoral fins are not blocked or gilled which facilitates escape movements (Horsfield and Turnpenny, 2011). Because a direct comparison between the two configurations has not been made, this experiment aimed to compare the effectiveness of angled bar racks with either horizontally or vertically oriented bars for diverting downstream moving fish. To address the biased focus towards salmonids/ eels, the potamodromous cyprinids chub (*Squalius cephalus*) and barbel (*Barbus barbus*) were selected. These species differ in body morphology (barbel being adapted to a benthic lifestyle), and tend to form shoals as juveniles (EA, 2004, Kottelat and Freyhof, 2007). Small groups of five individuals were released under the experimental conditions created. Two discharge regimes (‘High’ and ‘Low’) were used, each creating their own hydrodynamic conditions at the rack and bypass. The effect of a rack angle to the oncoming flow (45° and 30°) was tested under high discharge. Specific objectives of this study were to determine: (1) the flow fields created by the bar racks, (2) bar rack performance for chub and barbel under these settings, and (3) interspecific differences in behaviour that explain observed performance.

5.2 Materials and Methods

5.2.1 Experimental set-up

Experiments were carried out in a large recirculating flume (21.4 m long, 1.38 m wide, and 0.6 m deep) at the International Centre for Ecohydraulics Research (ICER), University of Southampton, UK. A centrally located 8.2 m long section of the flume was isolated upstream from the rest of the channel by a flow straightener (10 cm wide polycarbonate honeycomb-structured screen) and downstream by a 0.5 cm x 0.5 cm square mesh panel, both of which prevented the fish from escaping the experimental area (Fig. 5.1). The upstream section of the flume that was not part of the experimental area ensured a steady flow was established before reaching the flow straightener. The flume was illuminated with fluorescent lighting installed 2.5 m above the flume floor. Up to six cameras mounted 1.6 m above the channel floor recorded fish movements in the observation zone. This ranged from 50 cm upstream of the bar rack to the bypass entrance (Fig. 5.1). Blackout screens were installed on both sides of the flume to prevent visual disturbance to fish during trials.

Under treatment conditions one of four different bar racks was located between 2.0 and 4.3 m downstream of the flow straightener and placed against the true left side of the flume and connected to the bypass entrance on the right side. The minimal distance of 2.0 m fish had to move downstream was chosen to maximize encounters with the bar racks during trials. Either a 1.78 m or 2.52 m long, 0.5 m high rack with vertical or horizontal aligned bars was used, which resulted in an angle towards the oncoming flow (α) of 45°, or 30°, respectively, so that the sweeping velocity would be at least similar to (for the 45° racks) or exceed (for the 30° racks) the escape velocity to promote guidance (Larinier and Travade, 2002, Raynal et al., 2013b) (Fig. 5.1, 5.2). All bar racks had a 5 mm bar width and 10 mm bar spacing, with square, 2.5 cm thick support bars (Fig. 5.2), which resemble typical bar screens used in parts of the UK (EA, 2009). The width of the bypass channel was 14 cm, so that it received approximately 10% of total flume discharge conform earlier studies (Amaral et al., 2002, 2003), although different bypass dimensions have also been used. For instance, a 30 cm wide bypass was used in a study investigating European eel response to angled bar racks (Russon et al., 2010), but as a result the bypass received approx. 32% of the flow under 0.50 m s^{-1} upstream flow velocity, which is unsuitable from a water abstraction point of view. The bypass used here was separated from the rest of the channel by Perspex (4 m long, 50 cm high and 1 cm wide).

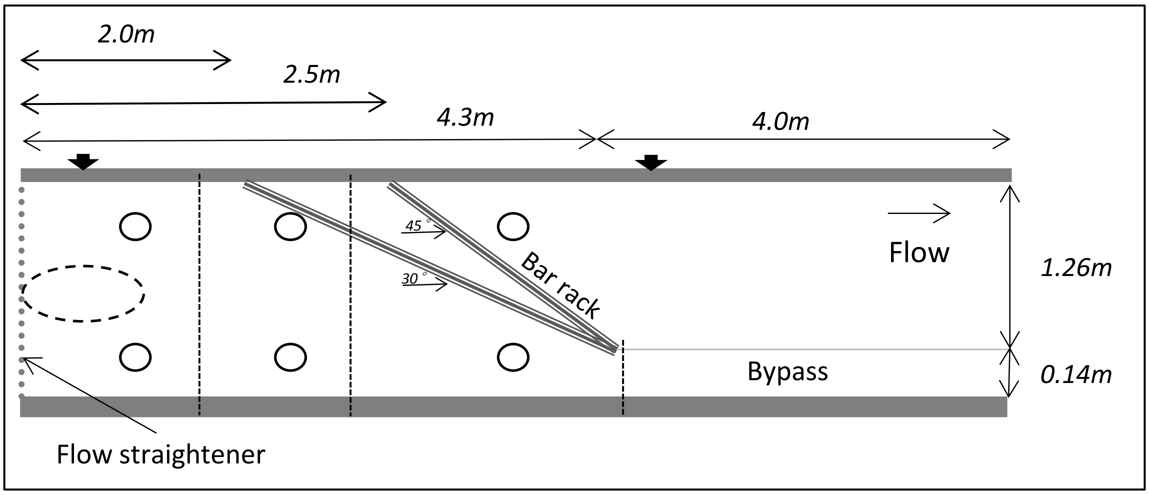

Figure 5.1. Plan view of an experimental section of a large recirculating flume at the ICER facility (University of Southampton). Each bar rack was placed against the true left side of the flume and connected to a bypass channel downstream. Closed circles represent locations of six overhanging cameras. The dashed circle represents the location of release. Thick black arrows denote locations of overhanging tube lights. Fish movements were recorded in the observation zone (dashed lines), which was smaller for short bar racks trials.

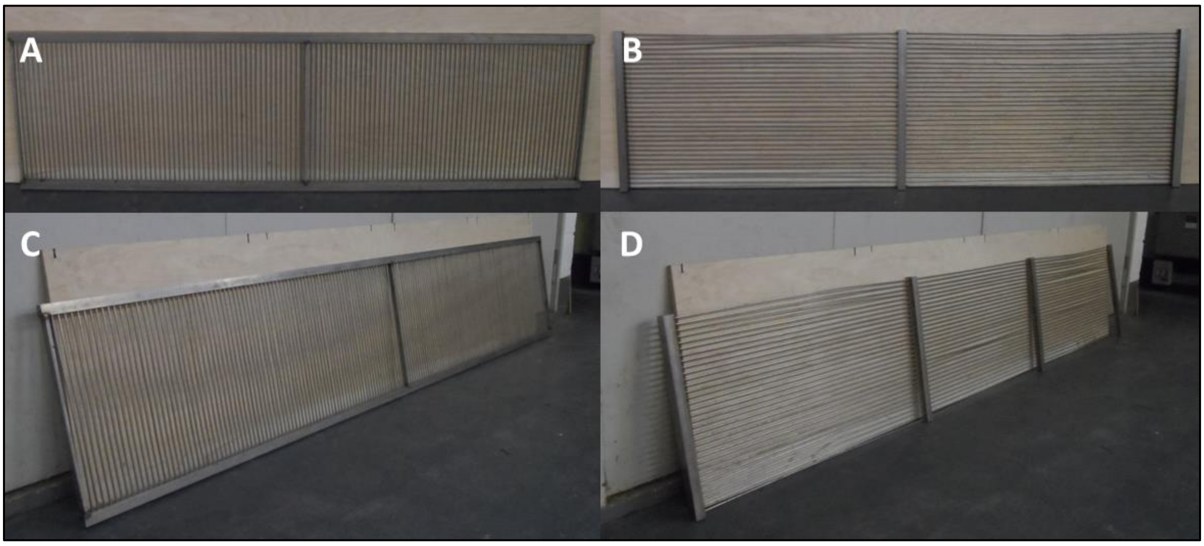

Figure 5.2. Bar racks used throughout this study. A) and B): short vertical and horizontal bar racks, respectively, used to test an angle of 45° to the oncoming flow. C) and D) long bar racks used to test an angle of 30° angle to the oncoming flow.

Two different discharge regimes were used, defined as low (L; 0.09 m^3 s^{-1}) and high (H; 0.15 m^3 s^{-1}). Both discharges were set by adjusting the pump valves and an overshot weir at the downstream end of the flume. Resulting mean ± S.D. flow velocities (mid-channel and mid-depth) were 0.19 m s^{-1} ± 0.01 and 0.36 ± 0.01 m s^{-1} under low and high discharge, respectively. Discharge levels are lower than the natural environment in which both chub and barbel occur, which includes fast flowing rivers with discharge up to 50 m^3 s^{-1} (Kottelat and Freyhof, 2007). Furthermore, under the high discharge regime, the corresponding escape velocity at the screen was below the recommended maximum value for coarse fish of 0.25 m s^{-1} (EA, 2009). The selection of discharge levels is therefore in agreement with what both species would normally encounter during their life cycle. Water depth (*D*) 1.5 m upstream of the start of the long rack was 0.38 m and 0.27 m under the low and high discharge, respectively. Fish behaviour was studied under six treatments: low horizontal (LH45), low vertical (LV45), high horizontal (HH30, HH45) and high vertical (HV30, HV45) (Table 5.1).

Table 5.1. Hydrodynamic conditions encountered by chub and barbel during downstream passage in a recirculating flume under low discharge (LH45, LV45) treatments in 2013 and high discharge (HH30, HH45, HV30 & HV45) treatments in 2014. *N* is the total amount of fish used per treatment.

Treatment	**Date**	**#Replicates chub/barbel**	**Mean (± S.D.) velocity upstream (m s^{-1})**	**Mean (± S.D.) velocity in middle of bypass (m s^{-1})**	**Mean (± S.D.) water temperature (°C)**	**Mean (± S.D.) total length chub/ barbel (mm)**	***N* chub/barbel**
LH45	5-8 December	10/10	0.19 (± 0.01)	0.21 (± 0.01)	11.1 (± 0.8)	85.3 (± 6.1)/ 93.1 (± 5.7)	50/50
LV45	9-12 December	10/10	0.19 (± 0.01)	0.19 (± 0.01)	10.3 (± 0.8)	83.9 (± 5.6)/ 89.3 (± 7.1)	50/50
HH30	17-18 February, 3 & 7 March	18/19	0.36 (± 0.01)	0.35 (± 0.01)	10.6 (± 0.7)	88.3 (± 7.5)/ 84.2 (± 7.1)	90/95
HH45	21,22 & 27 February, 5 March	16/19	0.36 (± 0.02)	0.37 (± 0.01)	10.9 (± 0.7)	86.2 (± 8.2)/ 81.7 (± 7.5)	80/95
HV30	19-20 February, 2 & 6 March	17/19	0.36 (± 0.02)	0.44 (± 0.02)	11.1 (± 0.6)	84.4 (± 7.2)/ 83.7 (± 8.4)	85/95
HV45	23, 24 & 28 February, 4 March	18/19	0.36 (± 0.01)	0.42 (± 0.01)	11.2 (± 0.7)	84.8 (± 6.7)/ 81.3 (± 7.6)	90/95

5.2.2 Experimental procedure

A total of 150 chub (mean total length (TL) and wet mass (M) ±S.D. = 84.8 ± 7.1 mm; 5.3 ± 1.4 g, respectively) and 150 barbel (mean TL ± S.D. = 91.0 ± 8.0 mm; mean M ± S.D. = 6.4 ± 1.6 g) were collected from a fish farm in Calverton, UK, (53°2'1.3" N, -1°3'7.0" W) on 12 November 2013. A total of 475 chub (mean TL ± S.D. = 86.2 ± 7.9 mm; mean M ± S.D. = 5.7 ± 1.7 g) and 475 barbel (mean TL ± S.D. = 83.0 ± 8.0 mm; mean M ± S.D. = 4.9 ± 1.3 g) were collected there on 5 February 2014 as well. Fish were transported to the ICER flume facility in sealed plastic bags filled with oxygen oversaturated water. All fish were maintained in three (2013) and four (2014) 3000 L outside holding tanks (mean and S.D. water temperature 7.0 °C ± 1.0 in 2013; and 7.4 °C ± 1.1 in 2014) in dechlorinated and oxygenated water for two weeks prior to use in trials. Water quality (pH, and levels of NH_3, NO_2^-, and NO_3^-) were monitored throughout the duration of the experiment, with 50% water changes when necessary. Chub were separated from barbel throughout the duration of the experiment. Fish were fed twice daily, at least 2 hours before use in trials.

All trials were conducted during hours of daylight. A total of 40 trials were conducted under the low discharge regime in the period 1-15 December 2013 (Table 5.1). Species was alternated daily, and rack configuration was changed after all associated trials with both species were completed. A further 152 trials were conducted under the high discharge regime between 15 February- 7 March 2014 (Table 5.1). As this experiment lasted longer and required more fish, species was alternated between trials. Treatments were randomly tested for two consecutive days, and randomised until the end of the experiment in an attempt to utilize similar sized test subjects across treatments. In spite of this and random selection of test fish at the beginning of trials, mean TL differed among treatments (chub: ANOVA $F_{5,474} = 4.27$, $p = 0.001$, being higher under HH30 compared to LV45, HV45 and HV30; barbel: Kruskal-Wallis $H = 92.86$, $df = 5$, $p < 0.001$, being higher under the low compared to the high discharge treatments (Table 5.1). However, since differences in TL were mostly small (less than 1 cm) and all test fish were capable of passing through the bar racks, the differences were not deemed conflicting for the objectives of this study.

Throughout each trial day, a total of 40 chub or barbel were randomly selected from the indoor holding tank and transported to 150 L containers filled with aerated flume water for a minimum of one hour. Prior to the start of each trial, five fish were randomly selected from this container and placed into a rectangular mesh (length: 53 cm, width 33 cm, height 20 cm) container in the upstream part of the flume for a minimum of twenty minutes to acclimate to the flow field. Each trial commenced when they were netted out and carefully released in the middle of the upstream part of the experimental area which they could volitionally explore. Trials lasted until all fish were downstream of the bar rack, or after 1 h had elapsed. At the end of each trial fish were removed from the flume and measured and weighed. Each fish was used only once during the study.

5.2.3 Hydrodynamics

To identify whether racks with varying bar orientation created differences in hydrodynamic conditions upstream of the racks, along an eight-point transect in front of the racks, quantification of the flow field was obtained using an Acoustic Doppler Velocimeter (ADV) (Vectrino+, Nortek). Sampling distance was ~ 8 cm (1 BL) perpendicular away from each rack. Sampling location was the same for horizontal and vertical short racks, but differed between both long ones due to the presence of vertical support bars (Fig. 5.2). Sampling volume and frequency were set at 0.28 cm^3 and 50 Hz, respectively. Sampling depth was set to $0.2D$, $0.4D$ and

0.8*D* under both discharge regimes, but pilots indicated that both species tended to remain at the channel floor during downstream movements. At each discrete measurement point, three thousand velocity readings were obtained over a period of 60 s. Raw ADV data was filtered following the protocol by Cea et al. (2007) and the mean velocity vector (***V***) was calculated as:

$$V = \sqrt{\overline{u}^2 + \overline{v}^2 + \overline{w}^2}, \tag{1}$$

where $\overline{u}^2$, $\overline{v}^2$ and $\overline{w}^2$ are the mean velocities in the *x*, *y*, and *z* direction, respectively. ADV velocity data was used to evaluate the deflection angle ($\boldsymbol{\beta_1}$) sweeping ($\boldsymbol{V_s}$) and escape velocities ($\boldsymbol{V_e}$) at every measurement point:

$$\tan\beta_1 = \frac{v}{u}, \tag{2}$$

$$\beta_2 = \alpha - \beta_1, \tag{3}$$

$$V_s = V * cos(\beta_2), \tag{4}$$

$$V_e = V * sin(\beta_2), \tag{5}$$

where *α* is the angle of the rack with oncoming flow (Fig. 5.3).

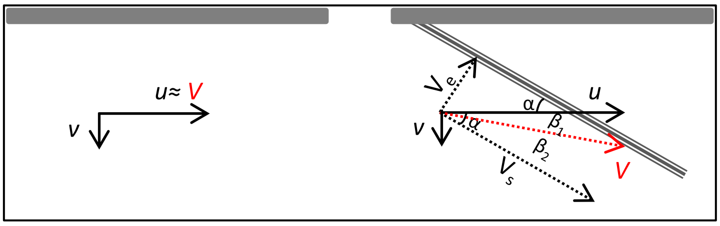

Figure 5.3. Velocity components at a measurement point 2.0 m away (left) and immediately in front of the bar rack (right). At 2.0 m upstream of the bar rack, the magnitude and direction of the mean velocity (**V**) mainly results from the x-component (**u**) as the y-component (**v**) is comparatively small. The presence of the rack diverts **V** by angle $\boldsymbol{\beta_1}$. **V** can be decomposed into a sweeping ($\mathbf{V_s}$) and escape ($\mathbf{V_e}$) component. These can be computed using $\boldsymbol{\beta_1}$ and **α** = 45° or 30°.

5.2.4 Bar rack performance

Every instance in which a fish entered the observation zone was categorised as an *approach*. Thereafter, three different routes of negotiating the bar rack were distinguished: (1) guided along the bar rack into the bypass, (2) through the rack (‘entrained’), or (3) along the true right wall without direct interaction with the rack. Fish were allowed to freely move up and down the experimental area and return upstream after negotiating the rack. As a result, multiple instances via the three routes were possible for an individual.

Percentage *bypassed* and *entrainment* per trial were defined as the proportion of released fish that, at the end of the trial, had entered the bypass or moved through the racks, respectively. For fish that returned and consequently negotiated the bar rack again, the first route was used in analysis.

Guidance efficiency per trial was defined as the number of times a fish entered the bypass as percentage of the number of times a fish approached.

Total numbers of fish that went through a bar rack (*entrained*), guided along it (*guided*), or impinged on it (*impinged*) were recorded per trial.

5.2.5 Fish behaviour

When moving downstream, individuals were deemed to belong to the same group when they were in the same (loosely) structured formation no more than 4 BLs apart (Hensor et al., 2003). *Group size* at moment of approach was recorded per trial.

Two distinct types of avoidance behaviour were categorised: 1) a return upstream after approaching the bar rack (*rejection*), and 2) halting downstream movement and staying in front of the screen following the first 30 s after approach (*holding station*). Number of *rejections* as well as the number of times fish displayed *holding station* were recorded per trial.

5.2.6 Statistical analysis

Tests of normality were performed using the Shapiro-Wilk statistic. Percentage data was transformed using the arcsine square root method prior to statistical analysis. Where normality of transformed percentage data failed, non-parametric tests were used. Count data was log-transformed in case of non-normality. When unsuccessful, either non-parametric tests were used, or parametric test results were reported together with bootstrapped (1000 iterations) 95% confidence intervals (CI) of the mean, to display general trends.

Bypassed, *entrainment* and *guidance efficiency* in each treatment were compared between species using *t*-tests or Mann Whitney U tests. *Guidance efficiency* was compared across treatments using Kruskal-Wallis tests.

Due to delay in bar rack availability, only the 45° angled bar racks could be tested under low flow. The effect of rack angle to the flow was separately assessed across the high discharge treatments. Where no differences were found, the data was pooled accordingly per species (e.g. HH30 + HH45). The influence of rack configuration and species on number of fish (1) *entrained*, (2) *guided*, (3) *rejections*, and (4) *holding station* were consequently assessed using bootstrapped (1000 iterations) univariate two-way ANOVA tests.

The number *impinged* was compared across treatments using Kruskal-Wallis tests, and between species using Mann Whitney U tests or Student's *t*-tests. Differences in *group size* were compared between treatments using Kruskal-Wallis tests.

Statistical data analysis was performed using IBM SPSS Statistics 20/22 software. A significance level of 0.05 was used.

5.3 Results

5.3.1 Hydrodynamics

Vector plots of ***V*** at the three sampling depths (0.2*D*, 0.4*D*, 0.8*D*) were highly similar and are shown only for the 0.2*D* case, as this is where fish of both species were predominantly found during trials (Fig. 5.4). Under low discharge, ***V*** was directed through the bar racks, regardless of orientation, at every sampling point (Fig. 5.4). Vector arrow length did not change with position towards the bypass, indicating that the amount of flow diverted was minimal. Under high discharge, diversion of ***V*** was also minimal, and ***V*** was not consistently directed to the bypass channel (Fig. 5.4). There were no discernible differences in the direction of ***V*** between horizontal or vertical bar racks, regardless of whether these were angled 45° or 30° to the oncoming flow. Under the HH45 and HH30 treatment, diversion of ***V*** seemed to take place where the vertical support bars were located (Fig. 5.2). It seemed that under all treatments, the direction of the mean flow was predominantly through the racks, and that neither a horizontal nor vertical bar rack was better in diverting flow effectively towards the bypass.

Analysis of the sweeping and escape velocities at each rack further confirmed that little to no change in sweeping velocities occurred towards the bypass under both low and high discharge (Fig. 5.5A, 5.6A, respectively). Escape velocities show no clear patterns, but generally changed little in magnitude along the rack across treatments (Fig. 5.5B, 5.6B, respectively).

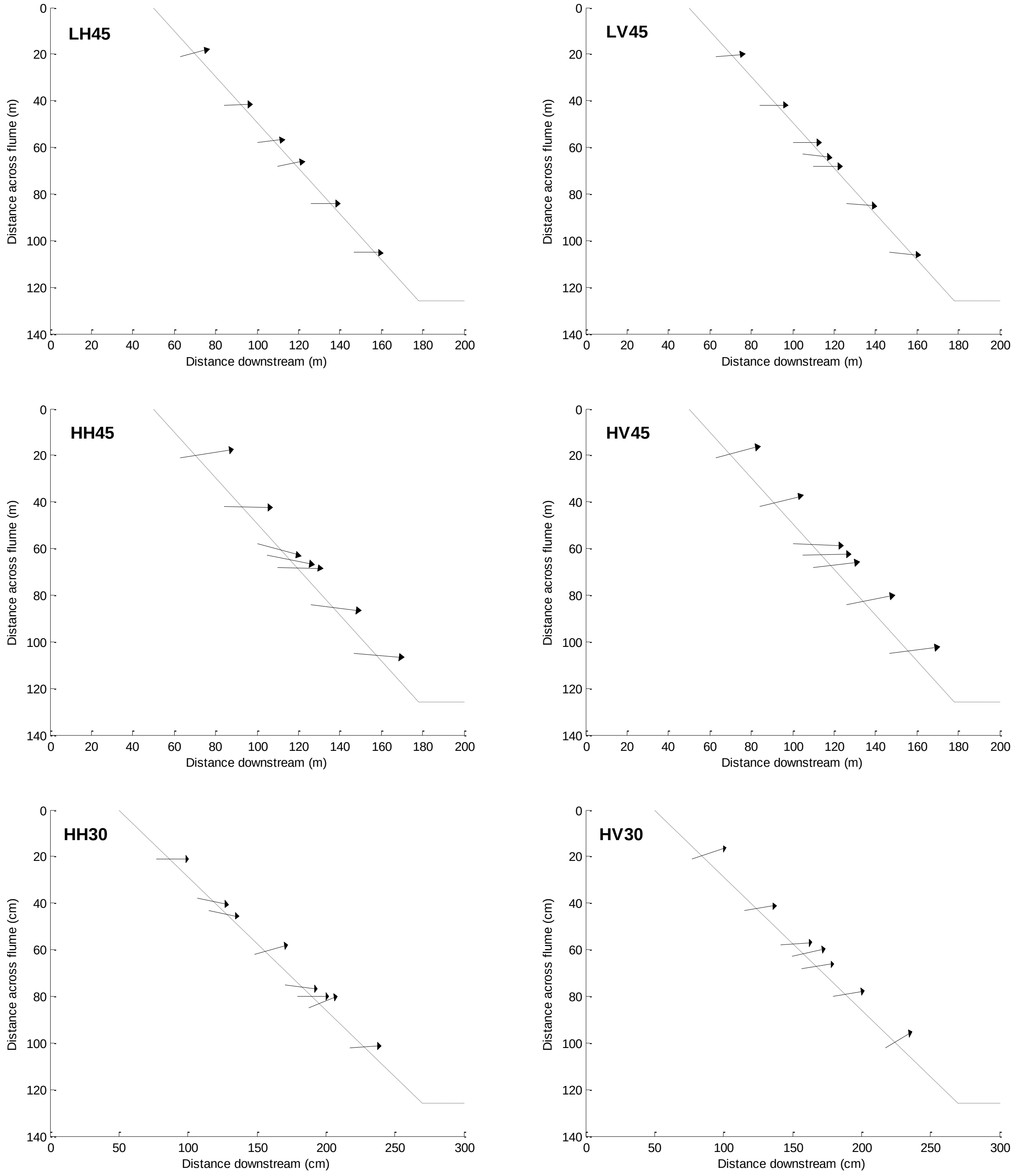

Figure 5.4. Quiver plots of the mean velocity vector (**V**) close to the channel floor (0.2D) in the vicinity of the bar rack under each treatment. Arrow length is scaled by mean **V** over a transect across the flume width, 2.0 m upstream of the rack in each treatment.

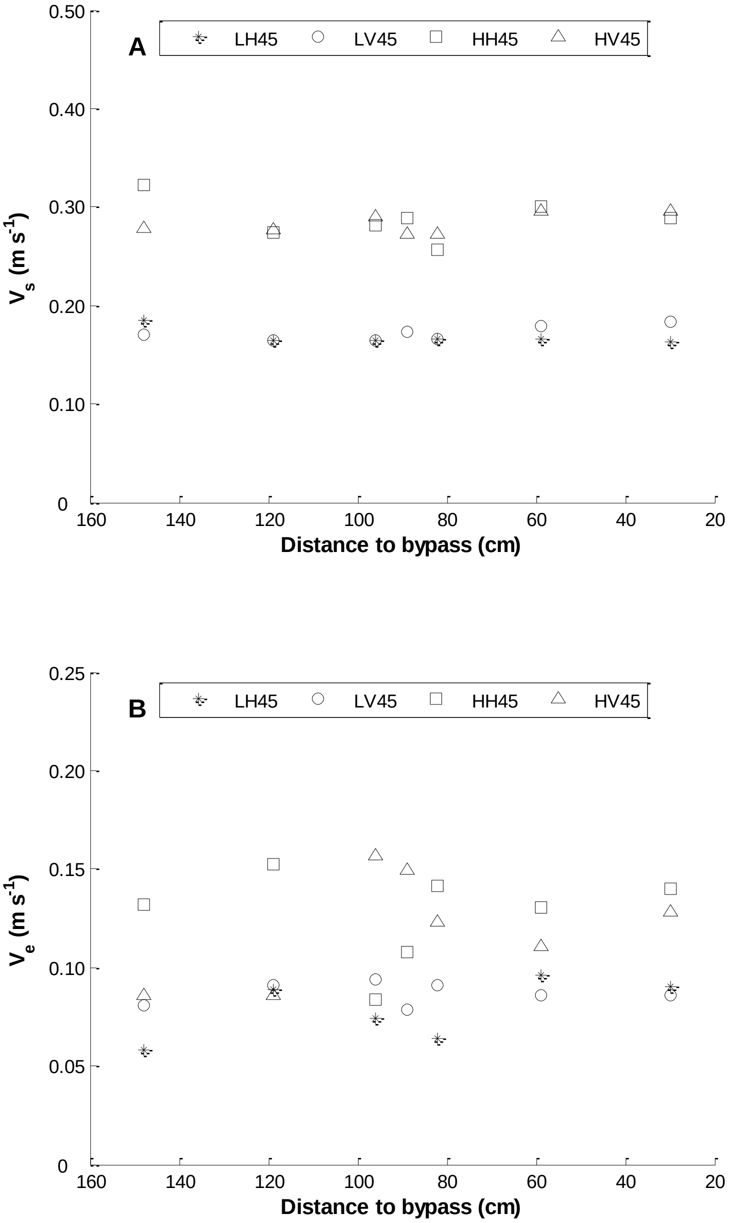

Figure 5.5. Flow velocities close to the channel floor (0.2D) upstream of angled bar racks under low horizontal/ vertical (LH45, LV45) or high horizontal/ vertical (HH45, HV45) treatments in a large flume. A) Sweeping velocity (**V_s**) along the 45° angled racks. B) Escape velocity (**V_e**) perpendicular to the 45° angled racks.

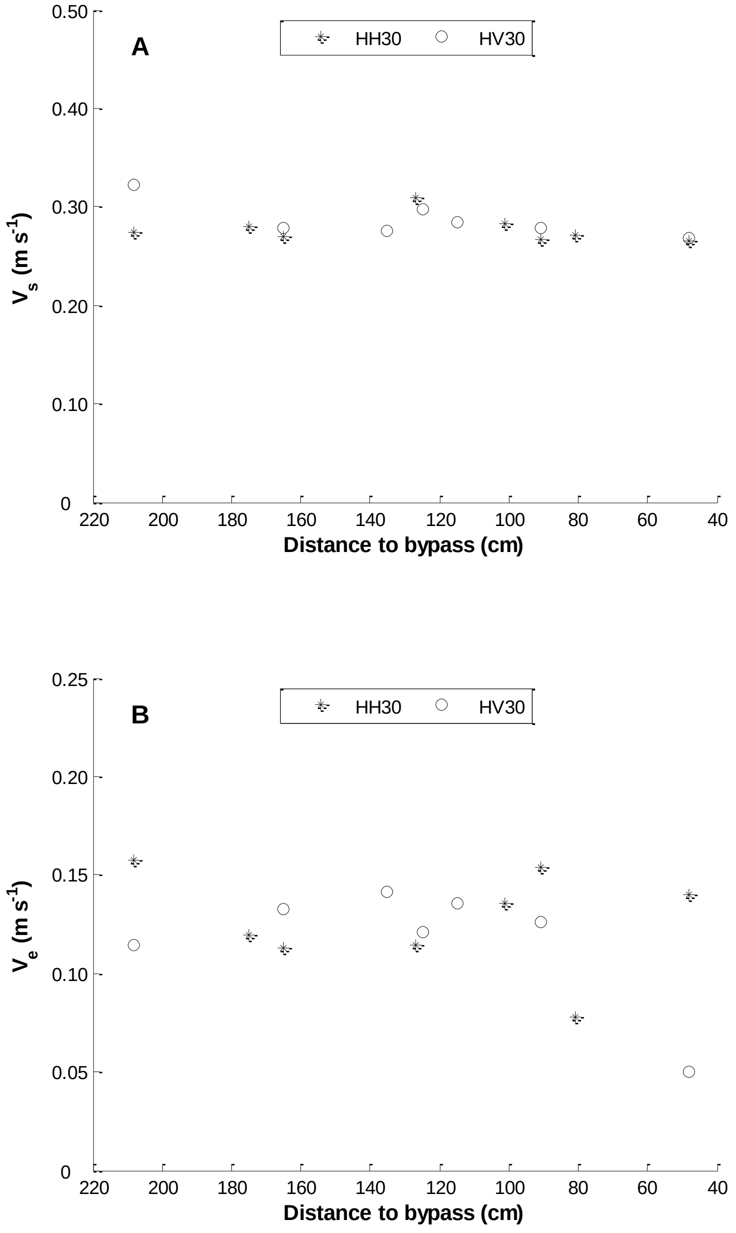

Figure 5.6. Flow velocities close to the channel floor (0.2D) upstream of angled bar racks under high horizontal/ vertical (HH30, HV30) treatments in a large flume. A) Sweeping velocity (**V_s**) along the 30° angled racks. B) Escape velocity (**V_e**) perpendicular to the 30° angled racks.

5.3.2 Bar rack performance

Across treatments, percentage *bypassed* and *entrainment* were higher for chub than for barbel (Table 5.2), indicating that of fish released, more chub than barbel negotiated the bar racks during the allotted time. This was indicated by the fact that almost half of barbel released (47.9% ± 10.3%) did not approach the bar rack at any time. Mean ± S.E. entrainment was 39.7% ± 5.1% and 22.4% ± 4.2% for chub and barbel, respectively, indicating that the bar racks were not very successful in preventing entrainment (Table 5.2). Percentage *bypassed* was significantly higher for chub than barbel when 30° racks were in place, and *entrainment* was significantly higher for chub under all but the HH30 and LV45 treatments (Table 5.3).

Table 5.2. Percentage of released fish that entered the bypass, entrained or did not approach bar racks under six treatments in a recirculating flume.

Treatment	% bypassed		% entrainment		% not approached	
	chub	*barbel*	*chub*	*barbel*	*chub*	*barbel*
HH30	54.7	32.1	23.3	29.5	22.1	38.5
HV30	42.2	22.1	34.9	7.4	22.9	70.6
HH45	26.2	16.7	49.2	14.6	24.6	68.8
HV45	34.5	29.6	36.9	5.6	28.6	64.8
LH45	28.0	30.8	66.0	30.8	6.0	38.5
LV45	54.0	46.9	28.0	46.9	18.0	6.1
Mean	**39.9**	**29.7**	**39.7**	**22.4**	**20.4**	**47.9**
S.E.	**5.1**	**4.2**	**6.4**	**6.6**	**3.2**	**10.3**

Mean *guidance efficiency* across treatments was 21.3% for chub. It differed between treatments (Kruskal-Wallis: $H = 15.04$, $df = 5$, $p < 0.05$) (Fig. 5.7A), and was significantly higher under the HH30 (median = 38%) than LV45 (median = 9%), $p < 0.05$. For barbel, mean *guidance efficiency* was 24.8% across treatments and differed between treatments (Kruskal-Wallis $H = 11.29$, $df = 5$, $p < 0.05$) (Fig. 5.7B). It was significantly higher under LV45 (median = 49%) compared to HH45 (median = 0%) ($p < 0.05$). Interspecific differences in *guidance efficiency* were found under the LV45 treatment, being significantly higher for barbel than for chub (Table 5.3).

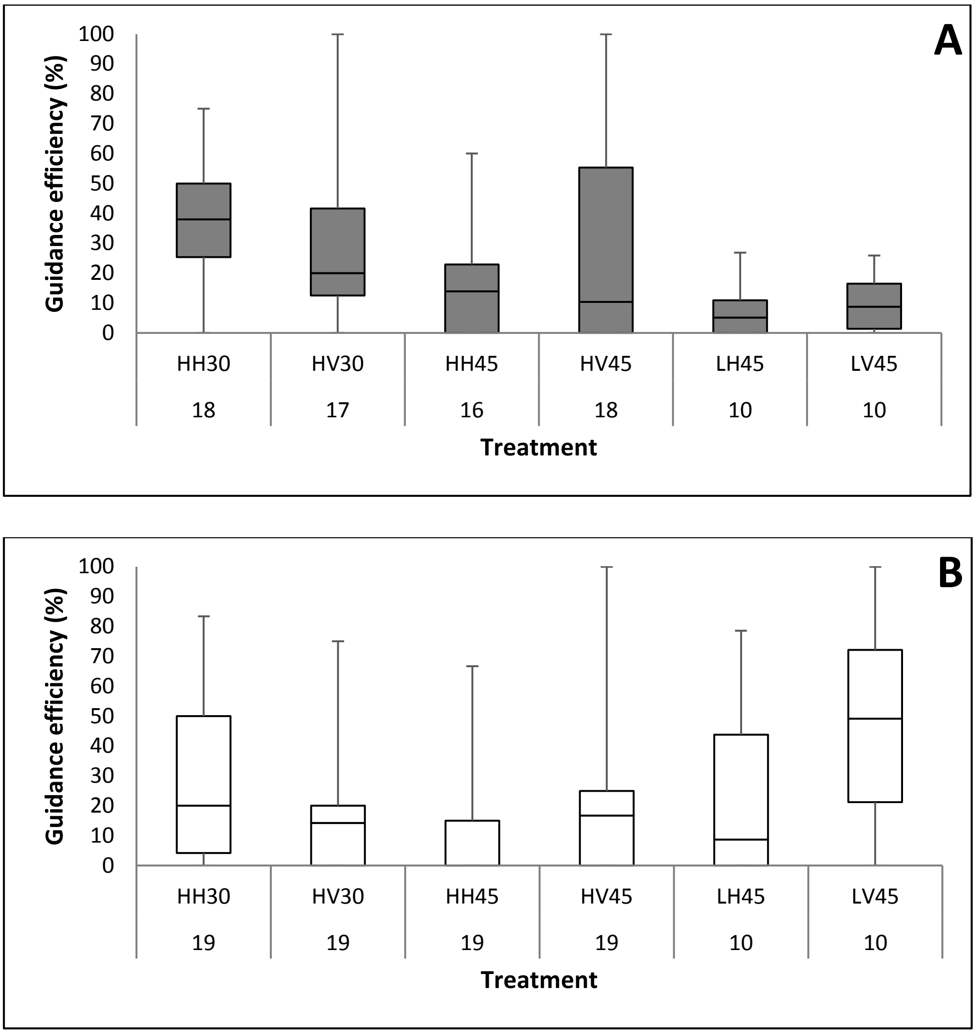

Figure 5.7. Guidance efficiency for chub (A) and barbel (B) under high horizontal/ vertical (HH, HV) or low horizontal/ vertical (LH, LV) treatments with 30° or 45° angled bar racks in a large flume. The number of replicates for each treatment is shown on the secondary x-axis. Boxes represent the IQR, and whiskers denote maximum and minimum values. Medians are denoted with a horizontal line and may overlap with IQR values.

Table 5.3. Interspecific differences in bypassed/ entrainment and guidance efficiency at bar racks in a recirculating flume.

Metric	Treatment	N	U	Z	*p*	Median chub (%)	Median barbel (%)
Bypassed	HH30	37	99.00	-2.22	<0.05	60	33
	HV30	36	91.50	-2.26	<0.05	40	20
Entrainment	HV30	36	58.50	-3.54	<0.001	40	0
	HH45	35	41.50	-3.86	<0.001	50	0
	HV45	37	68.50	-3.45	<0.01	29	0
	LH45	20	22.50	-2.13	<0.05	80	20
		df		t	*p*	Mean chub (%)	Mean barbel (%)
Guidance efficiency	LV45	18		-2.74	<0.05	10	47

Under high discharge, *entrained* was higher for chub than barbel (Fig. 5.8A). Neither rack configuration nor interaction had any effect (Table 5.4). Under low discharge, an significant interaction effect indicated that *entrained* was higher and lower for vertical compared to horizontal bar racks for barbel and chub, respectively (Fig. 5.8B). Rack configuration and species had no main effect (Table 5.4).

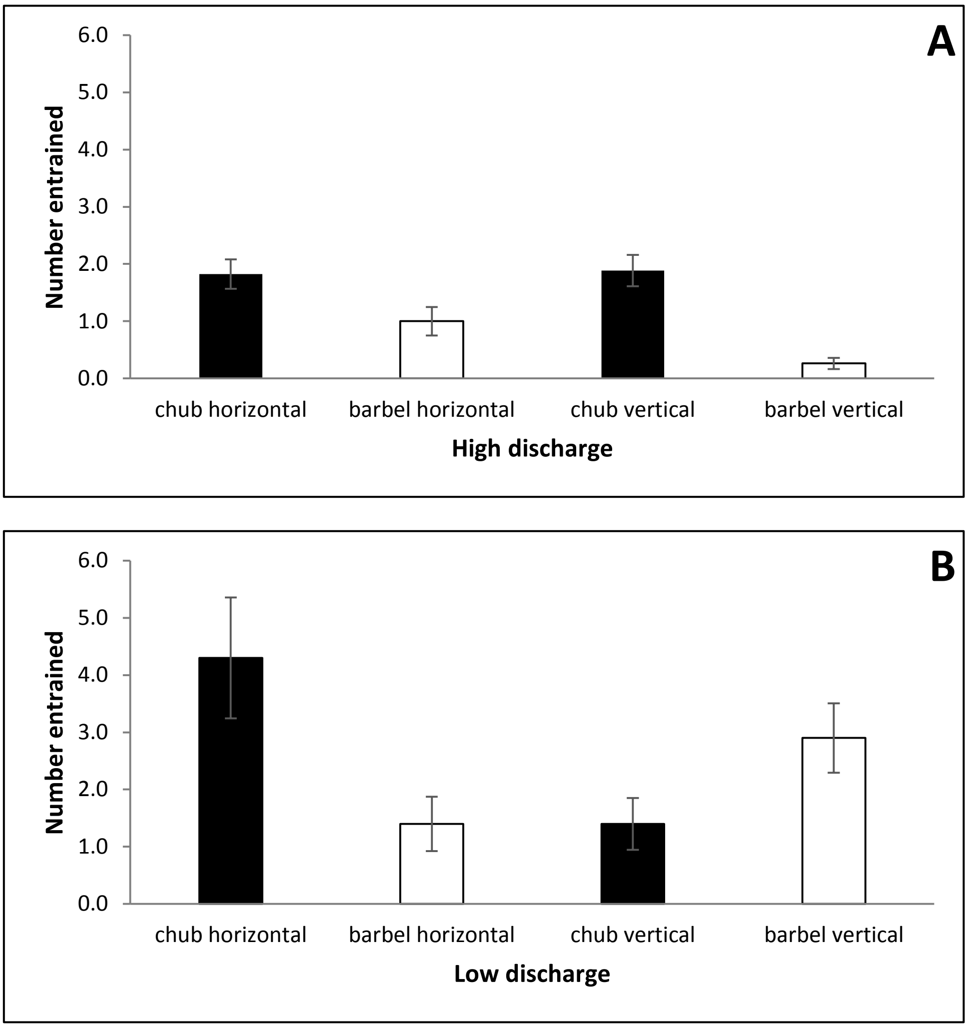

Figure 5.8. Mean (± S.E.) number entrained by bar racks under high (A) and low (B) discharge. For the high discharge treatments, data from those with a 45° rack was pooled together with those with a 30° rack, as angle had no effect.

Under high discharge, *guided* was significantly higher for vertical compared to horizontal bar racks and higher for chub than barbel (Fig. 5.9A), while an significant interaction between rack configuration and species was found (Table 5.4). Under low discharge, *guided* was significantly higher for vertical compared to horizontal bar racks (Fig. 5.9B). No species and interaction effect was found (Table 5.4).

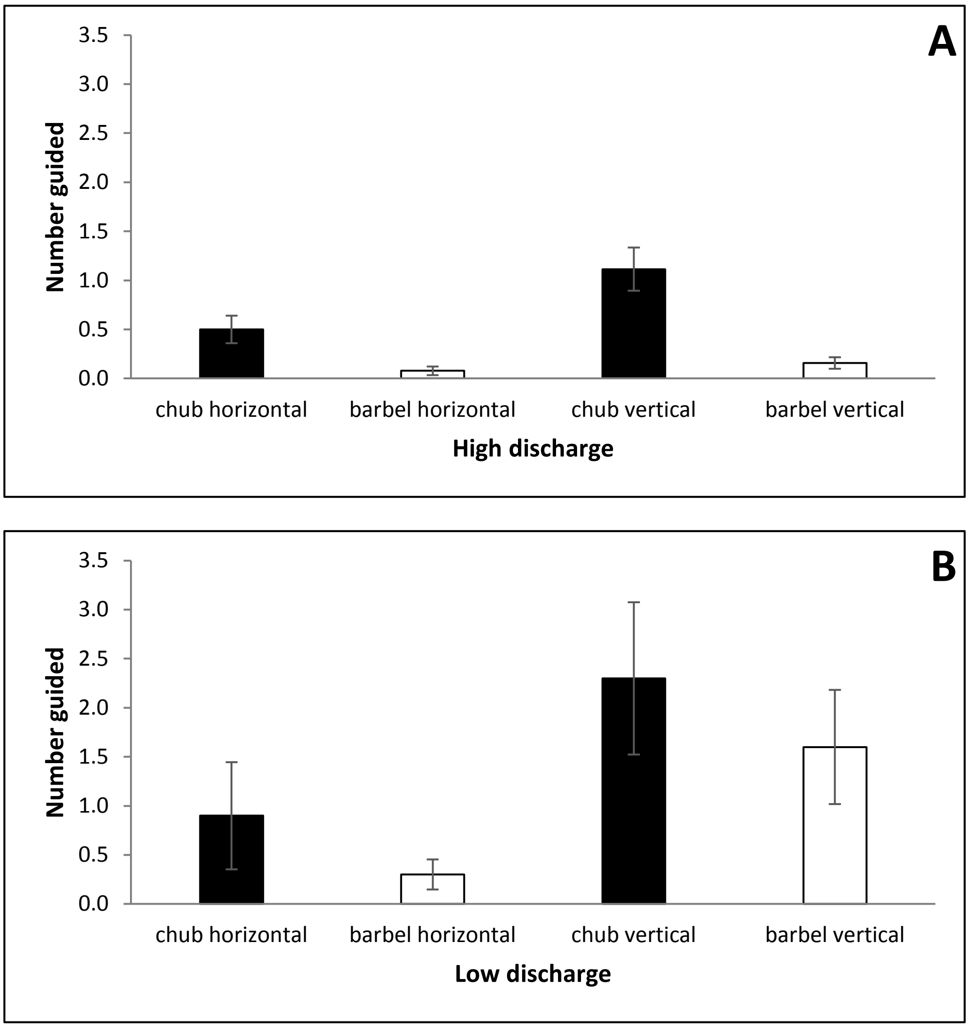

Figure 5.9. Mean (± S.E.) number guided by bar racks under high (A) and low (B) discharge. For the high discharge treatments, data from those with a 45° rack was pooled together with those with a 30° rack, as angle had no effect.

Impinged differed between treatments for chub (Kruskal-Wallis: *H* = 22.722, *df* = 4, *p* < 0.001). It was significantly higher under HH30 (median = 2.0) compared to HV45 (median = 0.0), *p* < 0.001 (Fig. 5.10). For barbel, number *impinged* was different between treatments (Kruskal-Wallis: *H* = 32.762, *df* = 5, *p* <0.001) (Fig. 5.10). It was significantly higher under LH45 (median = 8.0) and LV45 (median = 6.0) compared to HV45 and HH45 (medians = 0.0), all *p* < 0.001. Number *impinged* was different under HV30, being significantly higher for barbel (median = 3.0) than chub (median = 1.0) (Mann-Witney U: *U* = 83.00, *W* = 236.00, *Z* = -2.563, *p* = 0.01), under HV45, being significantly higher for barbel (median = 0.0) than chub (median = 0.0) (Mann-Witney U: *U* = 111.50, *W* = 282.50, *Z* = -2.403, *p* < 0.05), and under LH45, being significantly higher for barbel (median = 8.0) than chub (median = 0.0) (Mann-Witney U: *U* = 1.00, *W* = 56.00, *Z* = -3.786, *p* < 0.001).

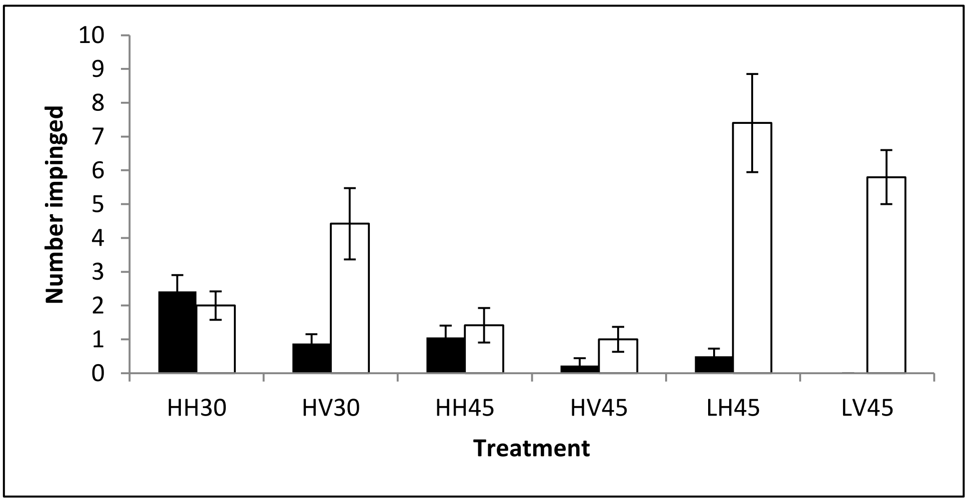

Figure 5.10. Mean (± S.E.) number impinged chub (black) and barbel (white) on bar racks under six treatments.

5.3.3 Fish behaviour

Both chub and barbel tended to stay close to the channel floor and approach the bar racks as individuals rather than as cohesive shoals, indicating variable *group size*. For chub, number of approaches as individuals did not differ across treatments, but it did for groups (Kruskal-Wallis $H = 36.29$, $df = 5$, $p < 0.001$), being significantly higher under LH45 (median = 10.5) compared to all high discharge treatments except HV30 (HH30: median = 3.0, $p < 0.01$, HH45: median = 2.0, $p < 0.001$, and HV45: median = 3.0, $p < 0.05$), and higher under LV45 (median = 13.8) compared to all high discharge treatments (HH30: $p < 0.01$, HV30: median = 7.0, $p < 0.01$, HH45: $p < 0.001$, and HV45: $p < 0.01$) (Fig. 5.11A). For barbel, number of approaches as individuals did not differ across treatments, but did for groups (Kruskal-Wallis $H = 21.69$, $df = 5$, $p = 0.001$), being significantly higher under LV45 (median = 2.0) compared to HV30 (median = 0.0, $p < 0.01$) and HV45 (median = 0.0, $p < 0.01$) (Fig. 5.11B).

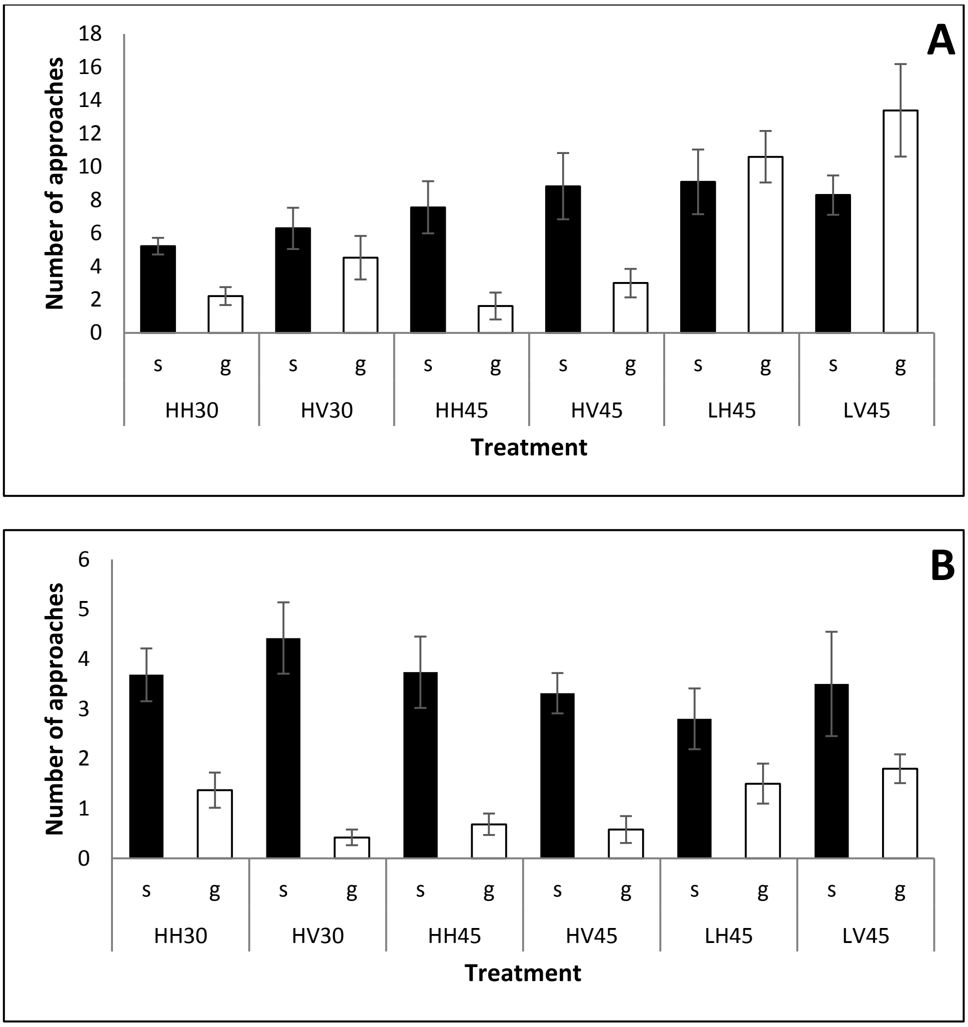

Figure 5.11. Mean (± S.E.) number of approaches as a single individual (s) or as a group (g) for chub (A) and barbel (B) under six bar rack treatments in a large recirculating flume.

Under high discharge, a significant interaction effect indicated that *rejections* were higher and lower for vertical compared to horizontal bar racks for chub and barbel, respectively (Fig. 5.12A). Chub rejected more than barbel, but rack configuration had no effect (Table 5.4). Under low discharge, chub rejected more than barbel (Fig. 5.12B). Rack configuration had no effect and there was no interaction (Table 5.4).

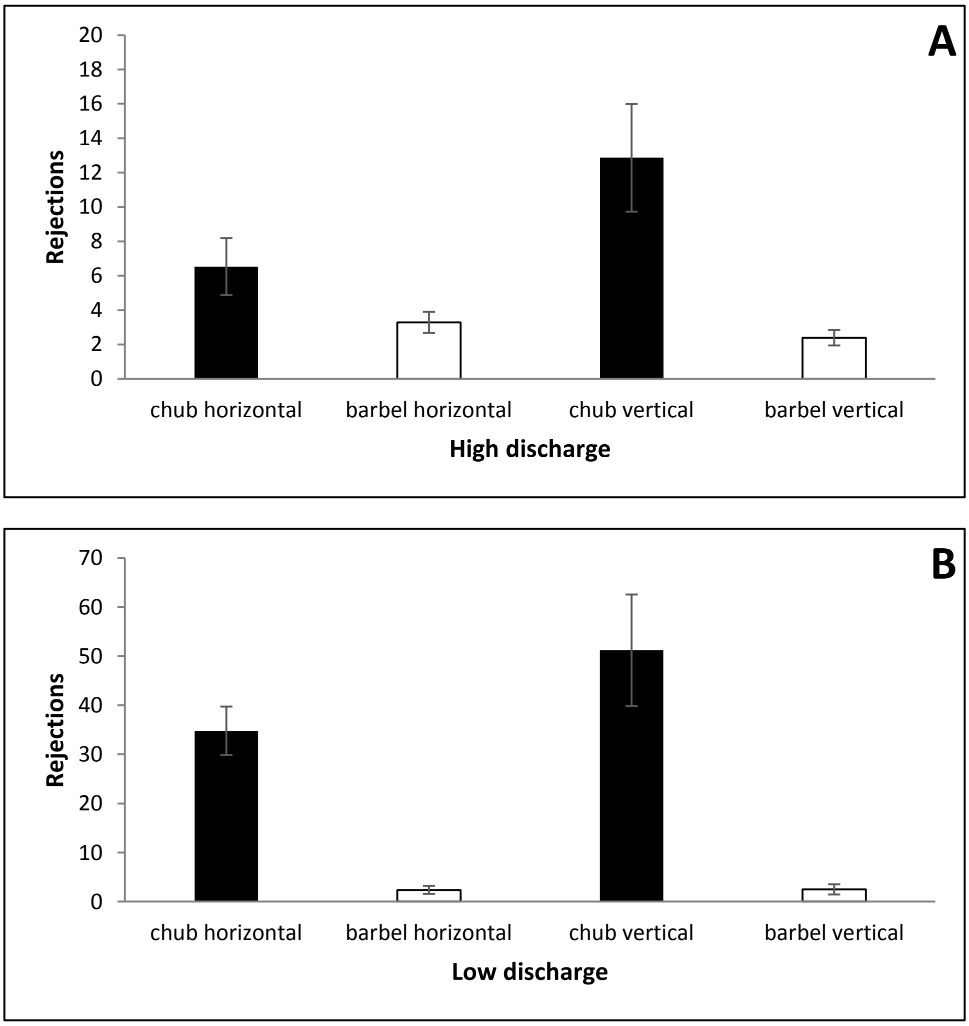

Figure 5.12. Mean (± S.E.) rejections to bar racks under high (A) and low (B) discharge by chub and barbel. For the high discharge treatments, data from those with a 45° rack was pooled together with those with a 30° rack, as angle had no effect.

Under both discharge regimes, *holding station* was significantly higher for chub than barbel (Fig. 5.13A, B). No main effect of rack configuration or interaction was found (Table 5.4).

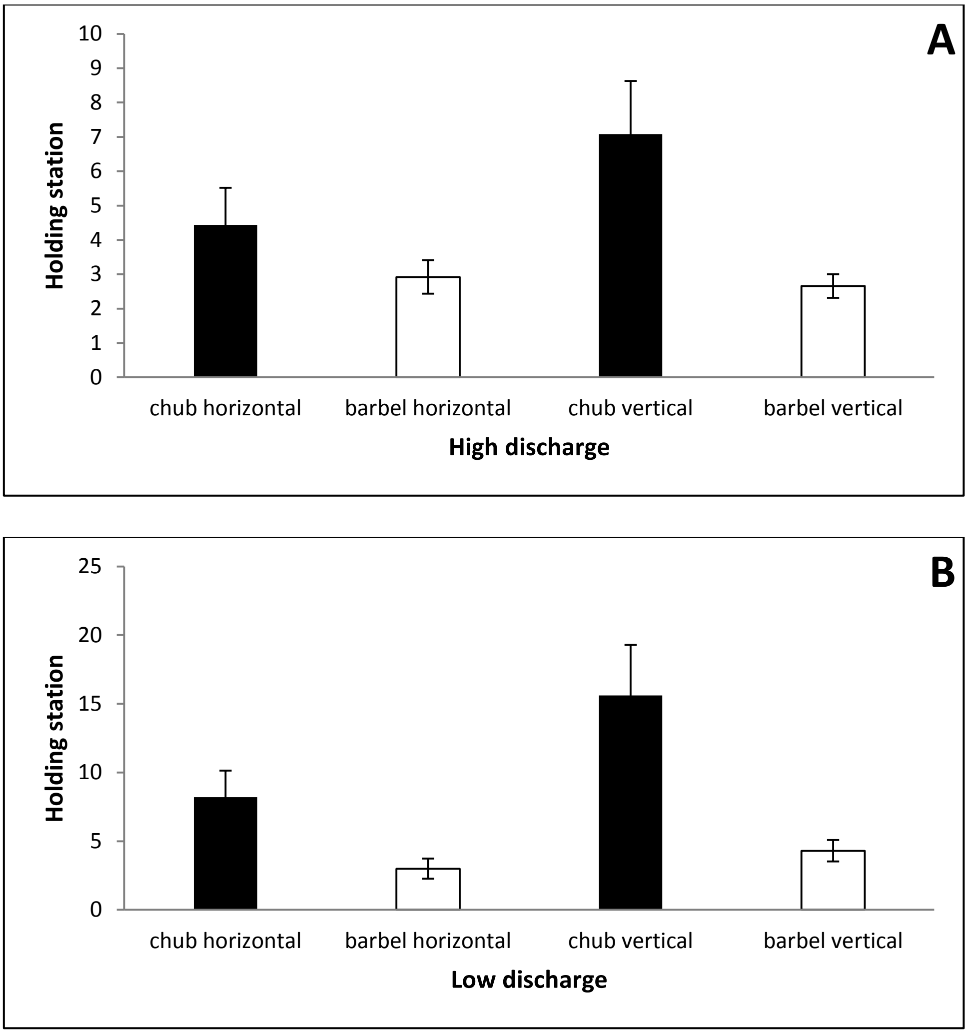

Figure 5.13. Mean (± S.E.) number of fish holding station to bar racks under high (A) and low (B) discharge. For the high discharge treatments, data from those with a 45° rack was pooled together with those with a 30° rack, as angle had no effect.

Table 5.4. Bootstrapped two-way ANOVA results, comparing the influence of rack type and species on the number of fish entrained or guided, and avoidance response to bar racks in a recirculating flume. Data from the high discharge treatments were pooled together by rack type. Tests showing significant results are indicated by *, and the 95% confidence intervals of the mean in that case are reported.

Dependent variable	**Discharge**	**Rack configuration**				**Species**				**Interaction**			
		df	***F***	***p***	**95% *CI* of the mean**	**df**	***F***	***p***	**95% *CI* of the mean**	**df**	***F***	***p***	**95% *CI* of the mean**
(1) Entrained	High	1, 141	2.216	>0.05		1, 141	29.127	<0.001*	Chub [1.50, 2.24] Barbel [0.39, 0.93]	1, 141	3.108	>0.05	
	Low	1, 36	1.027	>0.05		1, 36	1.027	>0.05		1	10.142	<0.01*	Chub-hor [2.00, 6.60] Barbel-hor [0.50, 2.36] Chub-ver [0.57, 2.36] Barbel-ver [1.67, 4.00]
(2) Guided	High	1, 141	6.972	<0.01*	Hor [0.15, 0.45] Ver [0.43, 0.87]	1, 141	27.528	<0.001*	Chub [0.55, 1.07] Barbel [0.05, 0.19]	1, 141	4.158	<0.05*	Chub-hor [0.23, 0.81] Barbel-hor [0.000, 0.18] Chub-ver [0.71, 1.57] Barbel-ver [0.05, 0.29]
	Low	1, 36	5.781	<0.05*	Hor [0.12, 1.27] Ver [1.10, 2.92]	1, 36	1.340	>0.05		1, 36	0.008	>0.05	
(3) Rejections	High	1, 141	2.429	>0.05		1, 141	15.453	<0.001*	Chub [6.44, 13.38] Barbel [2.16, 3.656]	1, 141	4.293	<0.05*	Chub-hor [3.66, 10.12] Barbel-hor [2.24, 4.62] Chub-ver [7.23, 19.66] Barbel-ver [1.57, 3.34]
	Low	1, 36	1.764	>0.05		1, 36	42.623	<0.001*	Chub [31.98, 53.15] Barbel [1.30, 3.71]	1, 36	1.722	>0.05	
(4) Holding station	High	1, 141	1.558	>0.05		1, 141	9.722	<0.01*	Chub [4.06, 7.74] Barbel [2.23, 3.42]	1, 141	2.232	>0.05	
	Low	1, 36	4.089	>0.05		1, 36	14.707	<0.001*	Chub [8.13, 16.04] Barbel [2.51, 4.65]	1, 36	2.010	>0.05	

5.4 Discussion

A variety of physical screens have been developed to aid the downstream movement of migrating fish past intakes (O'Keeffe and Turnpenny, 2005, Kemp, 2016). This study experimentally assessed the functioning of horizontal and vertical bar racks for guiding groups of two morphologically different cyprinid species under two discharge regimes in a recirculating flume. Although vertical bar racks guided more fish to the bypass than horizontal ones, due to high proportions of fish (both species) that passed through the racks, none of the tested rack and discharge combinations here proved successful in preventing this while guiding chub or barbel to the bypass.

Analysis of the mean flow velocity in front of each bar rack revealed that it was directed through them and not consistently diverted to the bypass, regardless of rack configuration, discharge regime or sampling depth. Sweeping velocities did not increase towards the bypass, indicating that an increasing transport flow towards the bypass, did not establish. These results are possibly due to the presence of round bars in the racks, as water flows well around such a shape. This is supported by a study by Tsikata et al. (2014), where the authors report that bar racks with round or streamlined edges induce lower head losses than with rectangular, ‘bluff’ edges under a variety of bar spacing and inclination angles with oncoming flow.

Mean guidance efficiencies were below 25% for each species, reflecting a loss of individuals that entrained or approached often before entrance into the bypass. The proportion of fish released that bypassed was similar to entrainment. In guidance efficiency, only one interspecific difference was found, being significantly higher for barbel than chub under LV45. No significant differences in the number of entrained or guided fish was found between the long and short horizontal and vertical bar racks under high discharge. This allowed for the data from associated treatments to be pooled together and make a simplified comparison between rack configurations. The number of fish guided was significantly higher under vertical than horizontal screens. A possible explanation for this might be the presence of a support bar in the frame on the bottom of the flume, and although it could not be clearly observed on video (due to water surface distortion close to the rack), fish could have been guided by it. The used experimental setup did not allow for investigating whether the observed performance of the racks was due specifically to the fish's response to the flow field in front of the rack or to the structure itself. Therefore, the results presented in this Chapter are limited to the used settings, and further experimentation is required that investigates the response independent of either factor.

Under all treatments, approaches to the bar rack occurred more often as solitary individuals rather than as the group in which they were released. Furthermore, group approaches decreased under the high discharge compared to low discharge treatments. This suggests that shoal cohesion was not strong from the moment of release, and was also worse under high discharge. The breaking up of shoals when flows become too high has been noted before (e.g. Pitcher, 1973b, Lemasson et al., 2014), and could result less accurate or efficient movements for species that rely on social interactions to make directional decisions (Simons, 2004). In any case, individuals that remain upstream experience a delay that is energetically costly and decreases the chance of successful passage (e.g. Nyqvist et al., 2016). Further experiments are required to determine how shoal cohesion in juvenile chub and barbel is influenced by hydrodynamic conditions at or near bar racks, and how these can be manipulated to increase passage efficiency.

The observed performance of the bar racks can be ascribed to interspecific differences in behavioural response expressed by both species. Barbel are a benthic species and adapted to living on the bottom in flow conditions as opposed to chub which occur throughout the water column (Kottelat and Freyhof, 2007). This explains the low number of barbel approaching the racks during trials. Furthermore, barbel showed significantly less avoidance to the racks (rejections or holding station) compared to chub, came into contact with them often, which resulted in entrainment/ impingement. For similar benthic species (lake sturgeon, *Acipenser fulvescens*, and American eels, *Anguilla rostrata*) the addition of a bottom overlay which covered the lower 30 cm of the bar rack increased guidance efficiency (Amaral et al., 2002, Amaral et al., 2003), and further experiments should investigate if this could be a solution for barbel. Being less adapted to flow fields, chub significantly approached the racks more and showed stronger avoidance responses than barbel, both rejecting them and holding station more often. The high amount of interactions resulted in both higher numbers of entrained fish compared to barbel. This is likely due to the delay associated with the interactions and reduces fitness, as more energy is spent, and the mean flow mainly being directed through the racks. This matches observation for *Salmo salar* smolts, which are more likely to pass through turbines the longer they are delayed (Castro-Santos and Haro, 2003). A simple solution to reduce the high numbers of entrained fish would be to decrease bar spacing, however given the hydrodynamics in the vicinity of the bar racks, high numbers of impinged fish could be expected. Usage of flat bars on the other hand can promote a sweeping flow towards the bypass (Tsikata et al., 2014) that could aid in guiding fish along the racks under high velocities. How the orientation of flat bars and a sufficiently small bar spacing to eliminate entrainment influences hydrodynamics and fish screening will be further investigated in the next chapter.

Many different fish species are present in and migrating through riverine systems (Lucas and Baras, 2001), and as such there is a need for developing screening systems that are efficient in guiding multiple species/ life stages (Kemp, 2016). Accounting for all migratory and resident fish species in an experimental setting is difficult to realise. Here, it is shown here that the two cyprinid species with different body morphologies representing different life histories are not successfully screened. Future experiments should focus on identifying what flow conditions, and bar rack characteristics, are better suitable for diverting these species.

5.5 Conclusions

This study is the first to empirically compare the efficiency of horizontal and vertical bar racks for potamodromous cyprinid species in the context of downstream fish passage. It can be concluded that, under the tested experimental conditions, neither rack configuration was very successful (mean guidance efficiency <25%) in guiding juvenile chub or barbel of the tested size to a bypass channel. Significant differences in guidance efficiency between treatments were scarce, indicating poor overall performance. The underlying causes for this were an absence of sweeping flows towards the bypass as well as avoidance behaviours expressed by fish after approaching the racks. Without an established sweeping flow, fish were not swept to the bypass, but flushed through the racks with the direction of the mean flow. In addition, avoidance in terms of rejections and holding station was commonly observed (chub significantly more than barbel) meaning that interactions with the rack occurred often without successful passage.

Shoal integrity was significantly higher under low discharge and increased the chance of entrainment of individual fish as shoals broke up under high discharge. The results highlight the importance of considering both fish behaviour and hydrodynamics when attempting to construct efficient screening systems. Further research is warranted to improve screening systems for the species tested here under various flow conditions. In particular for barbel, which is an important indicator species for water quality (Britton and Pegg, 2011) and have been studied in the scope of fish passage (e.g. Silva et al., 2012, Silva et al., 2015), the results could aid in protecting this species in the future.

Acknowledgments

Dominika Mackiewicz (University of Southampton) conducted the ADV measurements as part of her MSc thesis. Special thanks to her for the assistance in this study.

Chapter 6: Effectiveness of horizontally and vertically oriented wedge-wire screens to guide downstream moving juvenile chub (*Squalius cephalus*) under experimental conditions

Summary

Physical screens are commonly installed to block fish from entering dangerous areas (e.g. intakes to hydropower turbines, irrigation canals, and fish farms), and to divert them to preferred alternative routes (e.g. bypass systems). In northern temperate regions, assessments of the functioning of screens has largely focused on diadromous species (e.g. salmon and eels), and ignored those with other life history characteristics. This study compared the efficacy of horizontally and vertically oriented wedge-wire screens to block and divert downstream moving groups of potamodromous chub (*Squalius cephalus*) to a bypass channel installed in a recirculating flume under two discharge regimes. Hydrodynamics differed between horizontal and vertical screens under both flows; the vertical configuration created a higher velocity gradient towards the bypass. Both screens successfully diverted chub, as over 90% of all the fish used across treatments eventually entered the bypass. However, guidance efficiency (the number of times a fish entered the bypass as percentage of the total number of approaches) was generally low (mean = 17.3 % across treatments, highest for the horizontal screen under low discharge [25.3%]). This was due to less avoidance (holding station or upstream retreat) to the hydrodynamic conditions created by the screen under this treatment. Horizontal performed better than vertical screens in guiding fish to the bypass, despite inducing lower sweeping velocities. Shoal cohesion was highly variable throughout trials, as individuals left and reformed shoals often.

Keywords: Fish passage, Cyprinidae, groups, wedge-wire screen, guidance efficiency.

6.1 Introduction

Widespread river engineering and high densities of infrastructure (e.g. dams and weirs) along European waterways reflect a legacy of a long history of water resource development and management (Paish, 2002, Demirbas, 2007). According to the International Commission of Large Dams, there are over 55,000 large dams (>15 m high) present worldwide (ICOLD), and over half the large rivers in Europe are affected by them (Nilsson et al., 2005). Many thousands of smaller structures, such as weirs and sluices, further exacerbate the impacts (Lucas and Baras, 2001, EA, 2010). The effects of impoundments include the disruption of flow regime (first order), which alters channel morphology and physical and chemical processes (second order), and leads to shifts in ecological regimes (third order), including changes in community composition and species abundance (Petts, 1980, Kemp, 2016). Depending on the type of impounding structure, fish movements can be completely blocked or impeded, while fish that enter intakes may be lost (e.g. to irrigation and water supply systems), or risk injury and mortality if they pass through turbines (Larinier and Travade, 2002, Kemp, 2016). As longitudinal movements are essential to completion of the life cycle of many species (Lucas and Baras, 2001), habitat fragmentation as a result of river impoundment threatens the continued existence of many fish populations (Liermann et al., 2012).

Often driven by environmental legislation, the development of a variety of environmental impact mitigation technologies reflects attempts to protect fish at impounding river infrastructure (Kemp, 2016) For example, fishways and bypass systems are installed at barriers to help upstream and downstream moving fish negotiate them (Katopodis and Williams, 2012), while physical and mechanical screens are designed to block fish that would otherwise enter intakes, and guide them to safer alternative routes, such as bypass channels (Taft, 2000, O'Keeffe and Turnpenny, 2005). However, previously published research on such technology has tended to focus more on fish passage than on the screens, with some notable exceptions (e.g. Gessel et al. (1991), Skalski et al. (1996) for salmonid smolts (*Oncorhynchus* spp.) in North America, and Russon et al. (2010), and Calles et al. (2013) for eel (*Anguilla anguilla*) in Europe). Furthermore, those studies that evaluate the effectiveness of screens often do so for diadromous species of economic importance (salmonids) or those considered threatened (e.g. eels), while benefits for the wider fish community are infrequently considered (Williams et al., 2012).

Evaluation of the efficiency of screens to guide fish to e.g. bypass channels (‘guiding efficiency’) yields variable results, likely reflecting differences in local site-specific characteristics (e.g. hydrodynamics) and variation between species and life-stage. Nevertheless, it is clear that when velocities close to the screen are high relative to swimming capabilities, fish may be injured through mechanical abrasion when making contact with the screen, or are killed if they become impinged and unable to escape (Swanson et al., 1998, Swanson et al., 2005, White et al., 2007). Some species, such as downstream moving European eel that exhibits strong thigmotactic behaviour, tend to show an avoidance response after contacting the screen (Russon et al., 2010), thus increasing the probability of injury, impingement, and mortality. Fish may also exhibit avoidance behaviour to the hydrodynamic conditions created at the bypass entrance, as observed for American shad (*Alosa sapidissima*) (Kynard and Buerkett, 1997) and Atlantic salmon (*Salmo salar*) (Larinier and Travade, 1999), thus increasing delay of passage at the structure. To improve the performance of screens there is a need to assess the current guidance of their design and operation. Design criteria is directed primarily at placement and the need to provide suitably high sweeping flow parallel to the face to enhance guidance towards a bypass, while minimising escape velocities perpendicular to the screen to reduce probability of impingement (EA, 2009). As a result, it is advised that screens should be placed at an angle of 45° or less to the oncoming flow (Courret and Larinier, 2008, Raynal et al., 2013b), while critical escape velocities vary depending on the target species of interest (e.g. 0.25 m s-1 for coarse fish, EA, 2009). Furthermore, the importance of fish behaviour in screen design and bypass design has also been recognised, with recommendations to avoid creating abrupt hydraulics transitions, such as rapid accelerations of velocity and turbulence that may induce undesirable avoidance behaviour (Williams et al., 2012).

Recently, the influence of bar orientation on screen effectiveness has received some attention, with the suggestion that self-cleaning is improved when a horizontal, rather than the traditional vertical, alignment is employed (Ebel, 2008, Ebel et al., 2015). However, it is proposed that horizontal screens may also be more conducive to escape of impinged fish, through less restriction of body movements in the horizontal plane (Horsfield and Turnpenny, 2011). Building on this assumption, the current study aimed to compare the effectiveness of wedge-wire screens oriented either in the horizontal or vertical dimension for downstream moving fish. To address the biased focus on species perceived to be of high economic or natural importance (salmonids and eels), a cyprinid, the chub (*Squalius cephalus*), was selected as the representative model for potamodromous (i.e. migrating within fresh water) species. In Europe, chub are widely distributed and is an important species for recreational angling. As chub are gregarious, especially in the juvenile stage (Kottelat and Freyhof, 2007), small groups of juvenile fish were released under the experimental conditions. Experiments were conducted under two different discharge regimes (‘High’ and ‘Low’), each creating their own distinct flow field at the screen and hydrodynamic gradient towards the bypass. Specific objectives of the study were to determine: (1) the flow fields created by wedge-wire screens oriented in the vertical and horizontal dimensions under both discharge regimes; (2) screen performance with respect to chub guidance under these settings; and (3) the behavioural aspects of chub explaining the observed screen performance.

6.2 Materials and Methods

6.2.1 Experimental setup

Experiments were conducted in a large recirculating flume (21.4 m long, 1.38 m wide, and 0.6 m deep) at the International Centre for Ecohydraulics Research (ICER), University of Southampton, UK. A centrally located 8.2 m long section was isolated upstream from the rest of the channel by a flow straightener (10 cm wide polycarbonate honeycomb-structured screen) and downstream by a 0.5 cm x 0.5 cm square mesh panel, both of which prevented fish from escaping the experimental area (Fig. 6.1). The flume was illuminated with fluorescent lighting installed 2.5 m above the flume floor. Five cameras mounted 1.60 m above the channel floor recorded fish movements in the observation zone, from 50 cm upstream of the screen to the bypass entrance (Fig. 6.1). Black screens were installed on both sides of the flume to prevent visual disturbance to the fish.

Under treatment conditions a 2.5 m long wedge-wire screen was placed at an angle of 30.3° to the oncoming flow and spanned a distance of 2.0 to 4.2 m downstream of the flow straightener between the flume wall and bypass entrance (Fig. 6.1; Fig. 6.2). The screen consisted of five 50 cm x 50 cm stainless steel wedge-wire panels (3 mm profile bar width and 6 mm spacing) which were rotated to alternate between horizontal and vertical alignment of profile bars. The width of the bypass was 10% of that of the flume channel and was longitudinally separated by a Perspex screen (4 m long, 50 cm high and 1 cm wide).

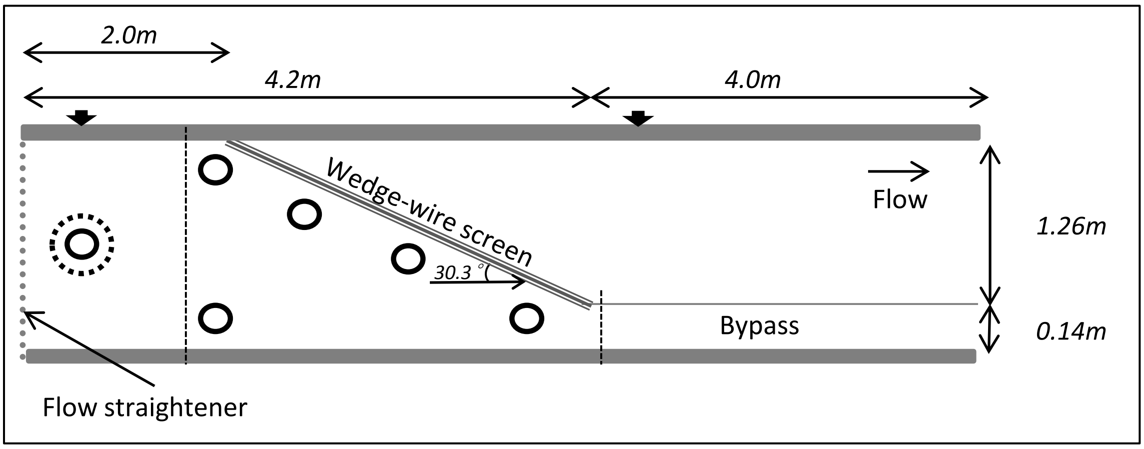

Figure 6.1. Plan view of the experimental part of a large recirculating flume at the ICER facility (University of Southampton). The wedge-wire screen was placed against the true left side of the flume, leading to the bypass downstream. Closed circles represent locations of overhanging cameras; the dashed circle represents the location of fish release. Thick black arrows denote locations of overhanging tube lights. Fish behaviour was recorded in the observation zone, indicated by the dashed lines.

Figure 6.2. Details of wedge-wire panels used throughout the study. A) Close-up of the side of a single panel illustrating the 3 mm profile bar width and 6 mm spacing; B) Plan view of a single 50 cm x 50 cm panel when profile bars are vertically oriented; C) wedge-wire screen (horizontal profile bar orientation) made up of a frame with five slotted panels in a large recirculating flume to create the plan view as shown in Fig. 6.1. The bypass channel was located at the far right.

Trials were conducted under two discharge regimes, defined as low (L - 0.09 $m^3 s^{-1}$) and high (H - 0.15 $m^3 s^{-1}$), and controlled by adjusting the centrifugal pumps and an overshot weir at the downstream end of the flume. Chub naturally live in faster flowing water up to 50 $m^3 s^{-1}$ (Kottelat and Freyhof, 2007) and under the discharges tested here, escape velocities were below the critical value~~s~~ of 0.25 $m s^{-1}$ which are in accordance with proposed for coarse fish (EA, 2009). Mean water depth 1.5 m upstream of the screen were 0.38 m and 0.27 m under low and high discharge, respectively. By altering the orientation of the panels within the screen, a total of four treatments were created: low horizontal (LH), low vertical (LV), high horizontal (HH) and high vertical (HV) (Table 6.1).

Table 6.1. Hydrodynamic conditions encountered by chub during downstream passage in a recirculating flume under two low flow (LH, LV) and two high flow (HH, HV) treatments. *N* is the total amount of fish used per treatment.

Treatment	#Replicates	Mean (± S.D.) velocity upstream (m s^{-1})	Mean (± S.D.) velocity in middle of bypass (m s^{-1})	Mean (± S.D.) water temperature (°C)	*N*
LH	14	0.17 (± 0.01)	0.24 (± 0.01)	10.7 (± 0.7)	70
LV	13	0.18 (± 0.01)	0.27 (± 0.01)	10.3 (± 1.1)	65
HH	12	0.36 (± 0.02)	0.49 (± 0.02)	11.1 (± 1.1)	60
HV	12	0.35 (± 0.01)	0.57 (± 0.02)	10.7 (± 1.4)	60

6.2.2 Experimental procedure

A total of 750 age 0+ chub were collected from the Environment Agency fish farm at Calverton, UK (53°2’1.3” N, -1°3’7.0” W) on 7 November 2014 and transported to the ICER research facility. Fish were maintained in two outdoor 2000 L holding tanks filled with dechlorinated and oxygenated water (mean + S.D. water temperature: 9.5 ± 2.9 °C) prior to use in the trials. Fish were acclimated to ambient indoor water temperatures by moving them to a 1000 L holding tank (mean ± S.D. water temperature: 10.7 ± 1.2 °C) one day before the trials commenced. Fish were fed twice daily. Water quality parameters (pH, NH_3, NO_2^-, and NO_3^-) were monitored throughout the duration of the experiment, with 50% water changes when necessary. Fish mean ± S.D. total length (TL) and wet mass (M) were 107.9 ± 5.7 mm and 11.3 ± 2.0 g, respectively. Mean ± S.D. water temperature in the flume at the beginning of trials was 10.7 ± 1.1 °C.

Fifty-one trials were conducted during hours of daylight between 29 November and 16 December 2014. A total of 40 chub were randomly selected each day from the indoor holding tank and transported to a 150 L container filled with aerated flume water for a minimum of one hour. Prior to the start of each trial, five fish were randomly selected from the container and placed in a circular mesh enclosure at the upstream end of the flume (Fig. 6.1) and allowed to acclimate for twenty minutes. Each trial commenced when the enclosure was raised and the fish released into the experimental area which they could volitionally explore. Each trial lasted until all five fish had entered the bypass, or in cases where they did not, after 2 h had elapsed. At the end of each trial fish were removed from the flume and measured and weighed. Each fish was used only once during the study.

6.2.3 Hydrodynamics

The combination of discharge and screen orientation created different fine resolution hydrodynamics created upstream of the screen under the four treatments. These were quantified using an Acoustic Doppler Velocimeter (ADV) (Vectrino+, Nortek - set with a 50 Hz sampling frequency, 0.28 cm^3 sampling volume, and recorded over a 60 s duration) at a depth of 5 cm above the channel floor, as pilot trials indicated fish tended to remain close to the channel floor when moving downstream. Raw ADV data was filtered following the protocol of Cea et al. (2007) and the mean velocity vector (***V***) was calculated as:

$$V = \sqrt{\overline{u}^2 + \overline{v}^2 + \overline{w}^2}, \tag{1}$$

where $\overline{u}^2$, $\overline{v}^2$ and $\overline{w}^2$ represent mean velocities in the *x*, *y*, and *z* direction, respectively. Spatial and vector maps of ***V*** under all treatments were visualised using Matlab (2014b). The deflection angle ($\boldsymbol{\beta_1}$) at which flow is diverted at the screen, and sweeping ($\boldsymbol{V_s}$) and escape ($\boldsymbol{V_e}$) velocities were calculated (Chapter 5, Fig. 5.3):

$$\tan \beta_1 = \frac{v}{u}, \tag{2}$$

$$\beta_2 = \alpha - \beta_1, \tag{3}$$

$$V_s = V * cos(\beta_2), \quad (4)$$

$$V_e = V * sin(\beta_2), \quad (5)$$

where α is the angle of the screen to oncoming flow (= 30.3°).

6.2.4 Screen guidance efficiency

When a downstream moving fish entered the observation zone, it was considered to have *approached* the screen area. Thereafter its routes to the bypass were categorised as either guided along: (1) the screen, or (2) the true right wall (without direct interaction with the screen). Fish were allowed to freely move up and down the observation zone and return upstream after *entrance* into the bypass channel. As a result, multiple approaches and entries per fish were possible.

Guidance efficiency per trial was defined as the number of times a fish entered the bypass as percentage of the number of approaches.

The number of fish guided along the screen (*guided*) was recorded per trial.

6.2.5 Fish behaviour

Whenever a fish left the observation zone by returning upstream after an approach without entering the bypass, it was deemed to have displayed a *rejection*. The total number of *rejections* was recorded per trial.

In the first 30 s following a successful approach to the screen, the number of times a fish *held station* in response to the screen was recorded per trial.

Fish were deemed to belong to a group when a loosely aggregated structure was formed in which individuals maintained a distance no more than 4 body lengths apart (e.g. Hensor et al., 2003). The number of times fish were moving either as a solitary individual or as part of a group (cases combined for a size of two up to five) was recorded in each trial at moment of *approach* and at *entrance* in the bypass.

6.2.6 Statistical analysis

A Shapiro-Wilk and Levene's test was used to test data for normality and homogeneity of variance. Percentage data and non-normal count data were arcsine square root and log transformed, respectively, prior to statistical analysis. Where normality was violated, and in the event that transformation was unsuccessful, non-parametric tests were used.

The influence of discharge and screen configuration (fixed factors) on (1) *guidance efficiency*, (2) *rejections*, and (3) the number of *approaches* as a solitary individual or group (dependent variables) were analysed using a univariate two-way ANOVA.

The influence on the number of fish *guided* (dependent variable) by the screen was evaluated by fitting a negative binomial generalised linear model (GLM). A Chi-squared test of independence was used to determine how the number of fish that *held station* differed between treatments.

The effect of treatment on the number of *entrances* in the bypass as a solitary individual or group was analysed using a Kruskal-Wallis test.

6.3 Results

6.3.1 Hydrodynamics

In general, the screens effectively diverted flow velocities (***u, v***) to the bypass, regardless of bar orientation and discharge (Fig. 6.3, 6.4). Under the four treatments, the magnitude of ***u*** increased along the screen towards the bypass, this was more pronounced when screen profile bars were vertically oriented (Fig. 6.3, LV, HV). The same trends were apparent for ***v*** (Fig. 6.3, bottom row), with more apparent diversion of ***v*** to the right, especially under the LV treatment. As a result, the gradient of ***V*** along a screen varied between 1.8 cm s^{-1} m^{-1} (LH) and 6.3 cm s^{-1} m^{-1} (HV) (Table 6.2). Vector plots of ***V*** showed that flow diversion occurred primarily where the screen met the channel wall (Fig. 6.4). High similarities between the profiles of ***u*** and ***V*** further suggested that the predominant direction of flow was in the same direction of ***u***, thus going through the screen (Fig. 6.4).

Table 6.2. Magnitude of ***V*** 5 cm above the channel floor at the start of the screen on the true left side of the flume and at the bypass entrance. The gradient is calculated by dividing the difference by the length of the screen (2.5 m).

Treatment	**Mean (± S.D.** $V_{screen\ wall}$ ***(cm s^{-1})***	**Mean (± S.D.** $V_{\text{bypass entrance}}$ ***(cm s^{-1})***	***Gradient ± S.D. along screen (cm s^{-1} m^{-1})***
LH	16.2 ± 0.5	20.9 ± 0.1	1.8 ± 0.2
LV	17.0 ± 1.2	23.2 ± 1.0	2.5 ± 0.6
HH	34.5 ± 1.5	47.4 ± 0.1	5.1 ± 0.6
HV	34.3 ± 1.1	50.0 ± 0.1	6.3 ± 0.4

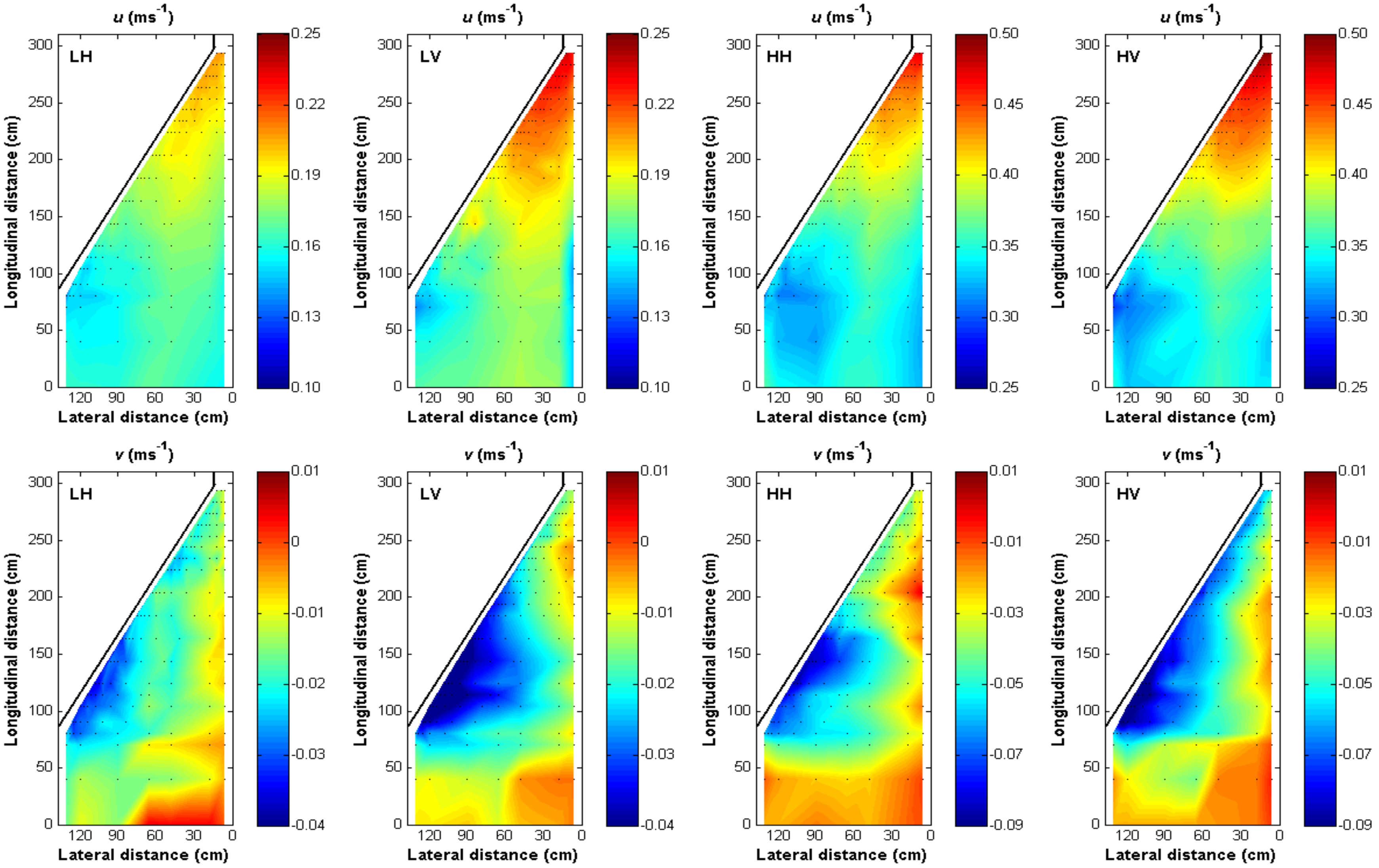

Figure 6.3. Colour density contour plots of **u** (top row) and **v** (bottom row), 5 cm above the channel floor upstream of an angled screen under two low (LH, LV) and high flow (HH, HV) treatments in which the orientation of a wedge-wire screen alternated between horizontal and vertical. The black line denotes the location of the screen and bypass channel, the black dots denote measurement locations. Note that the colour bars across treatments are similar, but the ranges of values vary depending on discharge.

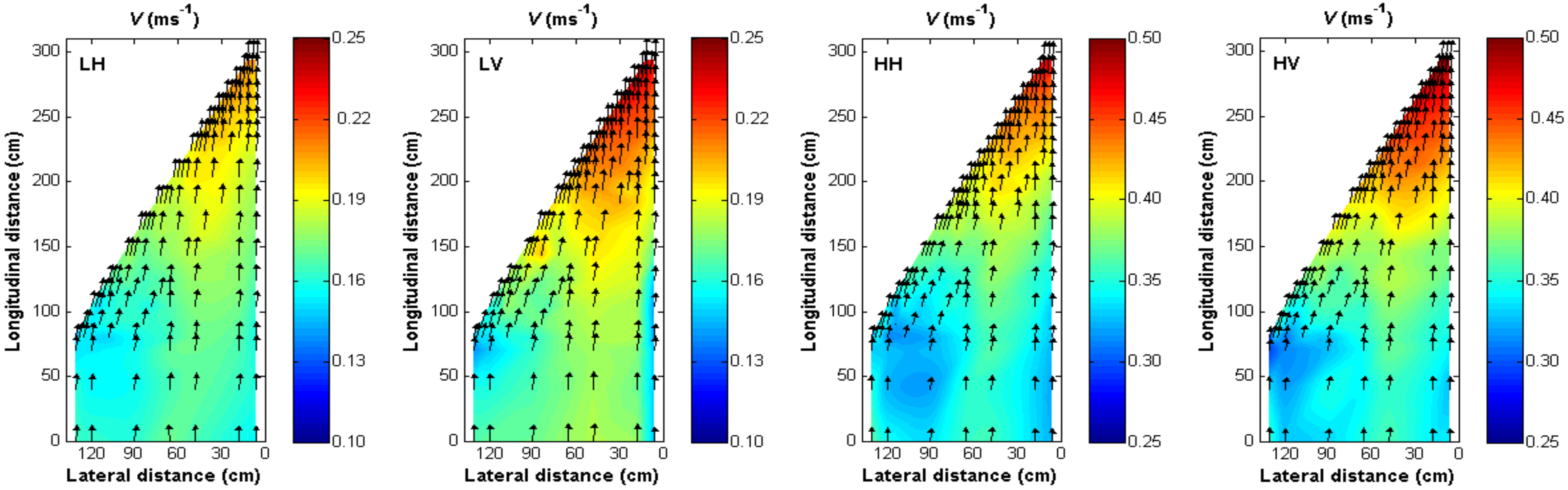

Figure 6.4. Colour density contour plots with vector plots overlaid of the mean velocity profile (**V**) 5 cm above the channel floor upstream of an angled screen under two low (LH, LV) and high flow (HH, HV) treatments in which the orientation of a wedge-wire screen alternated between horizontal and vertical. For illustration purposes, the screen and bypass channel are not shown here. Note that the colour maps across treatments are similar, but the ranges of values vary depending on discharge.

Under all treatments, $\boldsymbol{\beta_1}$ decreased towards the bypass entrance (Fig. 6.5A). The magnitude of $\boldsymbol{\beta_1}$ varied between 11-17° where the screen met the channel wall, and between 3-7° at the bypass entrance, without a clear difference between treatments. The low values for $\boldsymbol{\beta_1}$ confirm that flow diversion along the screen was generally low under each treatment. Under all treatments, $\boldsymbol{V_s}$ and $\boldsymbol{V_e}$ increased towards the bypass entrance and were lower under the low compared to the high discharge (Fig. 6.5B, C). Under low discharge, $\boldsymbol{V_s}$ varied between 0.16-0.19 m s^{-1} and $\boldsymbol{V_e}$ between 0.04- 0.09 m s^{-1}. Under high discharge, $\boldsymbol{V_s}$ varied between 0.31- 0.45 m s^{-1} and $\boldsymbol{V_e}$ between 0.08- 0.20 m s^{-1}. Horizontal screens induced slightly lower $\boldsymbol{V_s}$ than vertical ones (Fig. 6.5B). No discernible difference in $\boldsymbol{V_e}$ was evident between horizontal and vertical screens, regardless of discharge (Fig. 6.5C).

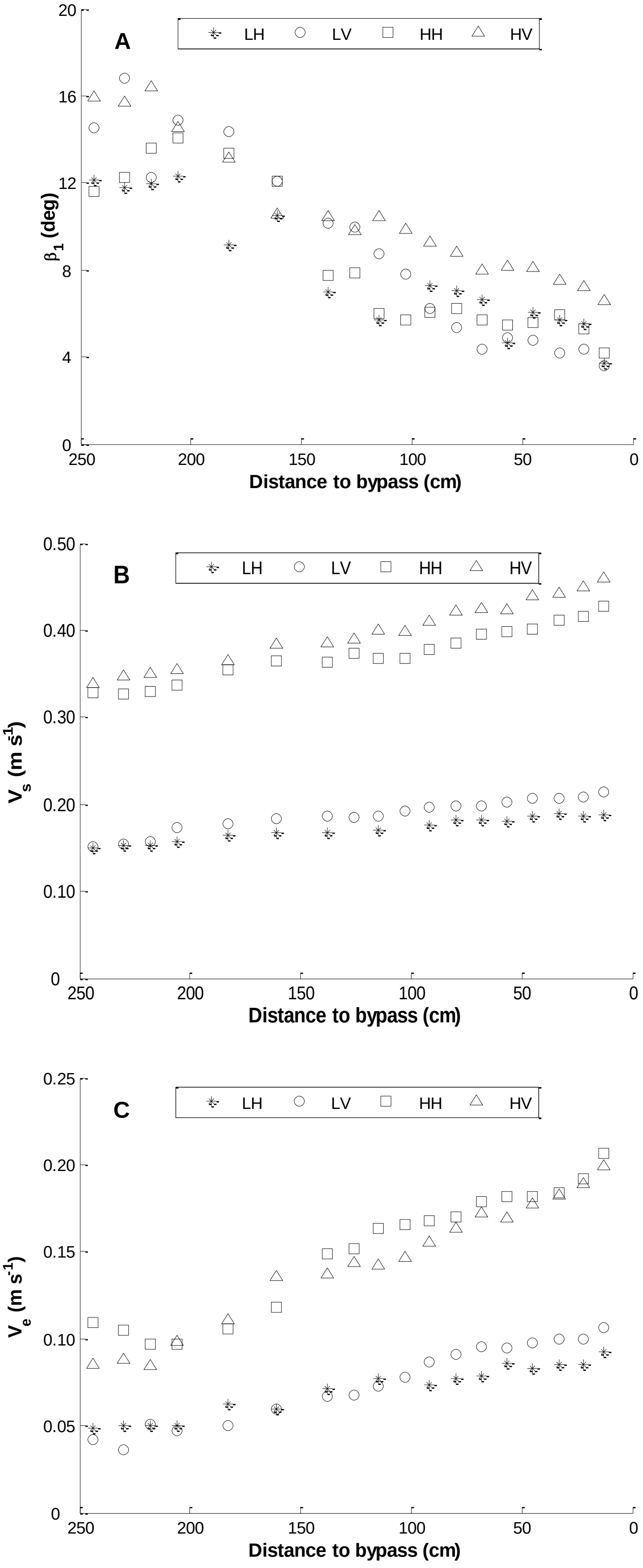

Figure 6.5. β_1 (A), **V_s** (B), and **V_e** (C) along the screen towards the bypass entrance for four treatments, measured at 5 cm above the channel floor.

6.3.2 Screen performance

Across treatments, screens successfully diverted chub, as over 90% of the chub released upstream eventually entered the bypass (LH: 98.6%, LV: 94.2%, HH: 86.7%, and HV 83.3%). *Guidance efficiency* was highest under the LH treatment (Fig. 6.6A). An significant interaction between discharge and screen configuration ($F_{1,47} = 5.92$, $p < 0.05$) indicated that a combination of these explained the observed differences. Without retaining a significant outlier in the HV treatment (Grubb's test $p < 0.05$), *guidance efficiency* was influenced by discharge, being significantly higher under low discharge ($F_{1,46} = 5.76$, $p < 0.05$), as well as the interaction effect ($F_{1,46} = 4.68$, $p < 0.05$).

The number of fish *guided* along the screen was highest under the LH treatment (*median*: 6.00, range 0 to 19) (Fig. 6.6B). Both elevation of discharge (decrease in *guided* of 0.531, 95% CI [0.258-0.992], $p < 0.05$) and change to vertically oriented screen (decrease in *guided* of 0.515, 95% CI [0.292-0.908], $p < 0.05$) were significant predictors for *guided*, based on a negative binomial GLM that performed better than the null-model ($p < 0.01$).

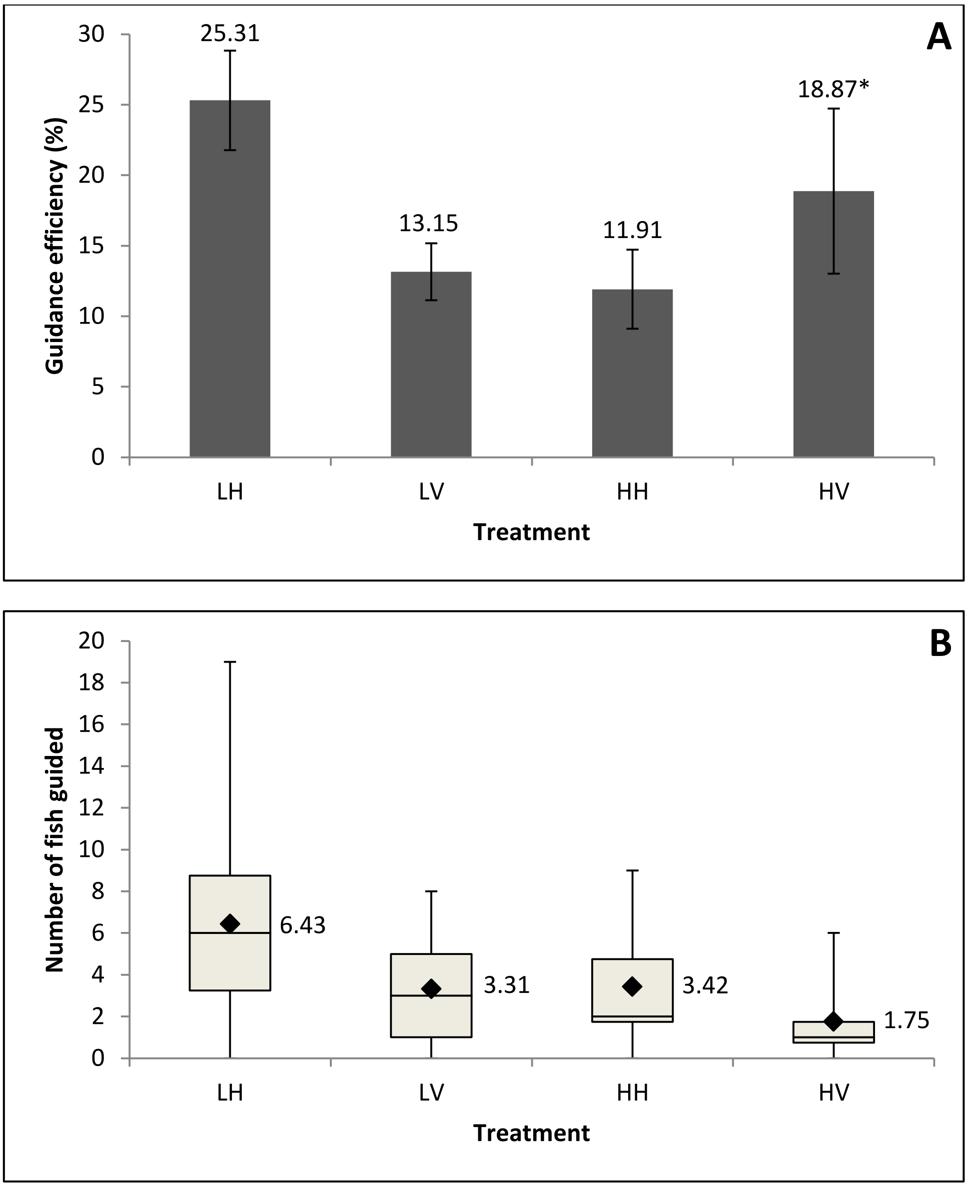

Figure 6.6. Guidance efficiency (A) and number of fish guided (B) under four screen treatments in a large recirculating flume. For the bar plot, the asterisk denotes the presence of a significant outlier in a treatment (see text). Error bars denote ± S.E. For the box plot, dots represent the mean (with values shown), horizontal lines the medians. Boxes represent the Interquartile Range (IQR), and whiskers denote maximum and minimum values.

6.3.3 Fish behaviour

Total *rejections* was lowest under the LH treatment (mean ± S.E.: 40.4 ± 5.3) (Fig. 6.7). The significant influence of both discharge ($F_{1,47} = 7.53$, $p < 0.05$), and its interaction with screen configuration ($F_{1,47} = 4.29$, $p < 0.05$), indicated that both factors explained the observed differences.

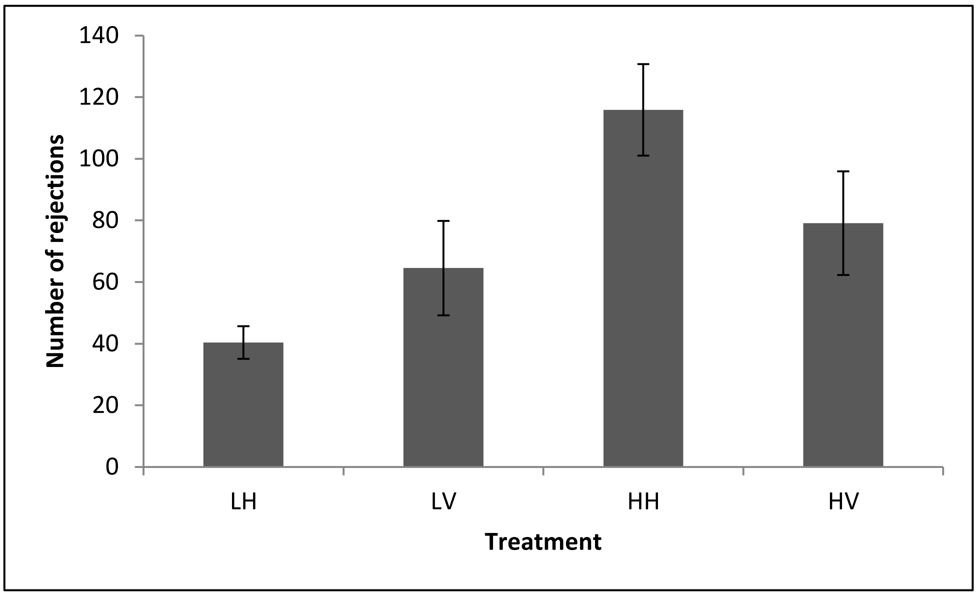

Figure 6.7. Number of rejections under four screen treatments in a large recirculating flume. Error bars denote ± S.E.

Group size was highly variable throughout trials, as individual fish left and re-joined the shoal often. Moreover, maximum group size decreased when individual fish entered the bypass whilst others were still upstream. In general, approaches and bypass entrances as individuals that had left a shoal was apparent across treatments (Fig. 6.8). The number of *approaches* was significantly higher under the high discharge treatments for both solitary individuals and groups ($F_{1,47} = 5.21$, $p < 0.05$ and $F_{1,47} = 11.55$, $p < 0.01$, respectively) (Fig. 6.8A). The number of *entrances* in the bypass differed between treatments for solitary individuals only (Kruskal- Wallis: $H = 17.20$, $df = 3$, $p = 0.001$), being significantly lower under the LV than HV ($p < 0.001$) and HH ($p < 0.001$) (Fig. 6.8B).

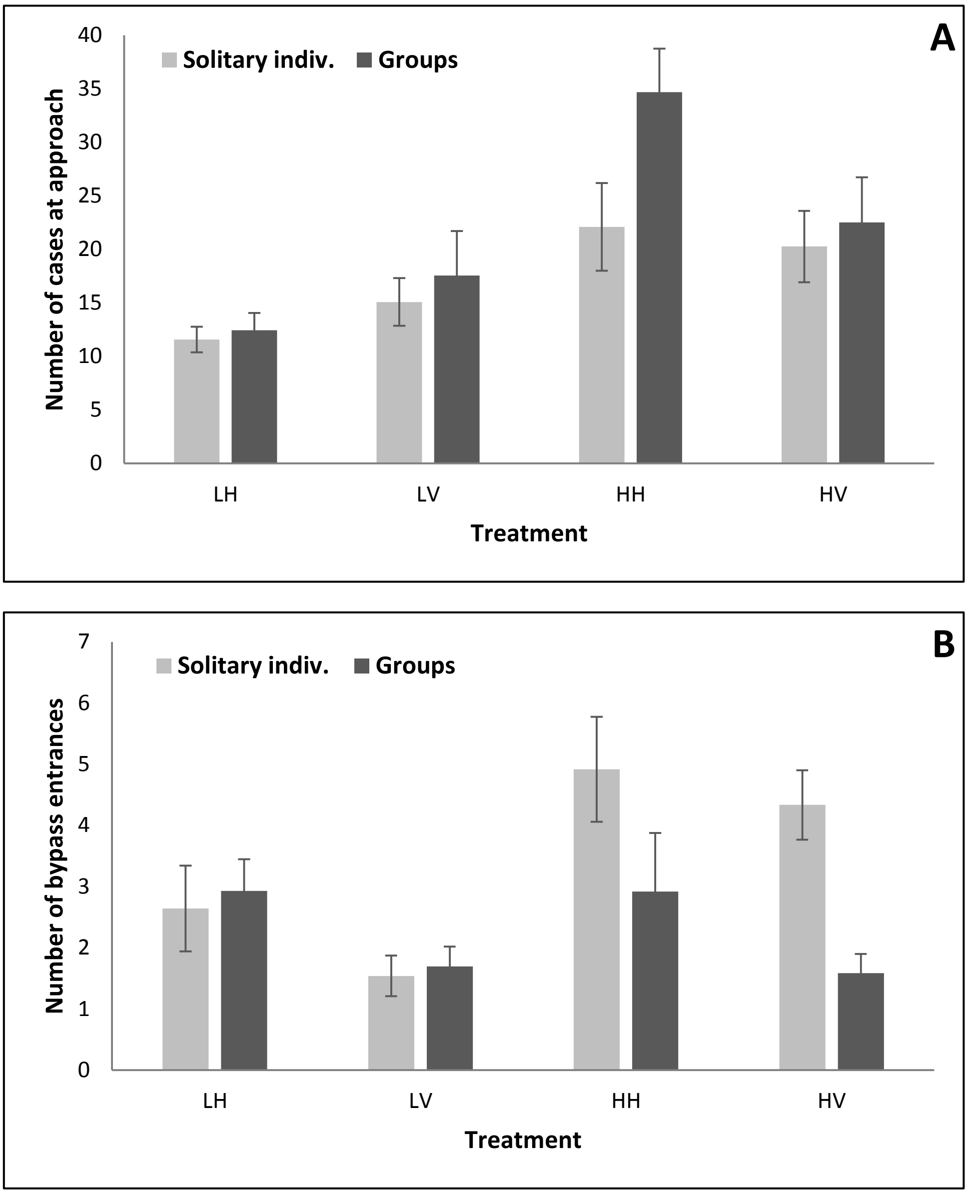

Figure 6.8. Number of approaches (A) and entrances into the bypass (B) as a solitary individual or group (combined for 2-5 fish) under four screen treatments in a large recirculating flume. Error bars denote ± S.E.

The number of fish that *held station* was influenced by discharge and screen configuration (X^2 (1,519) = 14.4, $p < 0.001$, $V = 0.17$), being lowest for the LH treatment ($n = 95$), followed by LV ($n = 115$), HV ($n = 117$), and HH ($n = 192$).

6.4 Discussion

Many freshwater fish species rely on longitudinal connectivity between habitats as part of their lifecycle, which calls for multi-species screening solutions at intakes (Kemp, 2016). For the first time, this study assessed the performance of horizontally and vertically oriented wedge-wire screens under two discharge regimes to divert juvenile chub to a bypass channel in an experimental setting.

There were clear hydrodynamic differences between horizontal and vertical orientations of the wedge-wire screens under both discharge regimes. While all screens created a specific velocity profile across the observation zone, their mean velocity gradient along the screen indicated that the vertical orientation diverted more water flow towards the bypass than horizontal ones. This resulted in higher sweeping velocities towards the bypass. Escape velocities were below 0.25 m s^{-1} under all treatments, conform the critical values proposed for coarse fish (EA, 2009). Results suggest that lower head losses could be expected with horizontal rather than vertical screens. These initial findings should be of interest to owners of intakes as this allows for more water to be abstracted (Clay, 1995, Raynal et al., 2013b).

A possible explanation for these observed hydrodynamic differences between horizontal and vertical orientations could be that flow separation by an individual vertical profile wire is more pronounced than of a horizontal one. The cumulative effect of these flow separations along a 2.5 m long vertical screen may then resemble the effect of Louver screens, whose specific design generates flow diversion and turbulence which aids in efficient guidance of fish to a bypass (Odeh, 1999, Shepherd et al., 2007). As this is highly speculative it requires experimental validation.

Over 90% of all chub released entered the bypass within the allotted trial time (2 hr), indicating that the screens were capable of diverting chub. However, guidance efficiency across treatments was <25% as chub required many approaches before entering the bypass. Highest guidance efficiency was found under low discharge with a horizontal screen in place (LH), despite the sweeping velocity being lowest overall for this configuration. Increasing the sweeping velocity does therefore not necessarily result in better guidance (suggested by Swanson et al., 2004). Furthermore, the number of fish guided along the screen (as opposed to along the true right wall) was higher with horizontal than vertical screens, and again highest under the LH treatment. These results demonstrate that both discharge and screen configuration explain screen performance, with horizontal ones being better. However, the used experimental setup did not allow for distinguishing between the fish's response to the flow characteristics and its response only to the physical nature of the wedge-wire screens. Experiments that isolate the two factors would provide better information as to what is more important. For instance, a setup with a similar flow field in front of a horizontal screen and vertical screen would be required to investigate the response to the wedge-wire screens. The results presented in this Chapter are limited to the used setup only.

Avoidance (followed by upstream retreat) exhibited by fish upon encountering areas of high flow acceleration as found in this experiment has been observed before (e.g. Kemp et al., 2005, Vowles and Kemp, 2012), and can lead to poor guidance efficiency (e.g. Kynard and Buerkett, 1997, Haro et al., 1998). In this study, rejections occurred more often under high discharge and were lowest under the LH treatment. In addition, upon encountering the screen, fish were least likely to hold station under this treatment. This behaviour can be seen as a form of avoidance (Vowles et al., 2014), and is often displayed by fish to maintain position in unsteady flows (Liao, 2007). When it occurs at screens however, it delays/ disrupts guidance with consequences for overall fitness, and predation pressure (Larinier and Travade, 2002). Our results demonstrate that the low rejection rates associated with the LH treatment explain the highest screen guiding efficiency found here.

Throughout trials, shoal cohesion was weak, as demonstrated by the relatively high presence of individual approaches and bypass entrances across treatments. Under high discharge, individual approaches and passes, and group approaches significantly increased, indicating that fission-fusion dynamics of shoals are more pronounced under this regime. Loss of shoal cohesion during downstream passage has previously been reported for groups of juvenile palmetto bass (*Morone chrysops* x *M. saxatilis*) negotiating Louver screens (Lemasson et al., 2014) and Atlantic salmon (*Salmo salar*) and American shad (*Alosa sapidissima*) groups at bypass weirs (Haro et al., 1998). It supports our finding that screen design and hydrodynamics are an important factor to consider in facilitating passage of shoals of fish. In the present study, it was not possible to determine which combination of screen and discharge was most efficient for the groups released.

6.5 Conclusions

Following on from the previous chapter, this study investigated the efficiency of wedge-wire screens with either horizontally or vertically aligned profile bars for guiding juvenile chub to a bypass channel. Under the tested conditions, the vertical screen diverted more flow towards the bypass. However, this did not imply more successful passage, as a significant interaction effect between screen and discharge indicated that in terms of guidance efficiency, the horizontal screen performed best under low, but not high discharge. The number of rejections, a proxy for avoidance, was also influenced by an interaction effect, and lowest for the horizontal screen under low but not high discharge. Under the tested low flow conditions, horizontal screens may be more efficient for diverting chub than traditional vertical ones. Results build on previous knowledge which has highlighted the importance of fish behaviour and screen hydrodynamics in the context of successful passage. Horizontal screens have already been installed in Germany (Ebel et al., 2015) and the results presented here could further aid in decision making during mitigation planning, for example in the UK, where thousands of water abstractions are present and need efficient screening (O'Keeffe and Turnpenny, 2005).

This study used chub, a species that lives in shoals when juvenile (Kottelat and Freyhof, 2007). Throughout trials however, shoal cohesion was weak and approaches occurred significantly more by individuals and groups under high compared to low discharge, as a consequence of more rejections at the screens. A better understanding of how shoal integrity is maintained in the vicinity of screens and under changing hydrodynamic conditions is therefore required for more efficient screening of shoaling species. This will help reduce the delay incurred by those left behind, which for instance can affect fitness or likeliness to succumb to predators (e.g. Ferguson et al., 2006, Schilt, 2007).

Chapter 7: Thesis discussion

Anthropogenic activities associated with the development of running water resources (rivers and streams) have resulted in a high density of barriers (e.g. dams and weirs) that fragment riverine waterways and affect freshwater fish species that migrate as part of their life history (Lucas and Baras, 2001). So, barriers are a major threat to freshwater fish diversity (Liermann et al., 2012), and if future exploitation of water from rivers and streams as a natural resource is going to continue while environmentally sustainable, adequate mitigation for migrating fish needs to be in place. Physical screens that enable downstream fish passage along barriers are frequently used but the efficiency of such screens is variable and sometimes unacceptably low (Gessel et al., 1991, Calles et al., 2013), reflecting difficulties in site characteristics and behavioural traits that differ between species and life stage. Social living has evolved throughout the animal kingdom, including in most fish species (Bourke, 2011, Shaw, 1978). Benefits that include cost sharing in anti-predatory and foraging strategies, or when on the move, reduction of energetic expenditure or enhanced navigation (Krause and Ruxton, 2002). Shoaling behaviour has not been thoroughly addressed in fish passage research. The experimental research presented in this thesis was undertaken to advance scientific knowledge to aid the improvement of fish screens design for gregarious, potamodromous fish. It focuses on four interrelated aspects:

1. *collective behaviour*: assessing the impact of flow velocity on shoaling fish as varying hydrodynamic conditions are induced by obstacles in the flow such as screens,

2. *screen hydrodynamics*: quantification of the flow field generated by different configurations of bar racks and wedge-wire screens
3. *screen performance:* effectiveness of the above screen types for guiding groups of juvenile cyprinids,
4. *behavioural response*: understanding the behavioural response of fish to the above screen types in relation to the observed performance.

This chapter discusses the key findings and limitations, and provides recommendations for future research.

The literature review revealed that collective behaviour emerges from the interactions and information transfer between members of the group, this has been a topic of high interest in science (Croft et al., 2008, Vicsek and Zafeiris, 2012). Using simple interaction rules based on attraction, alignment and repulsion, computer models have been successful in reproducing certain shoal features, such as oblong shape and frontal density (Hemelrijk and Hildenbrandt, 2008). The direct inferring of interaction rules from experimental data has been addressed recently (e.g. Herbert-Read et al., 2011), but the effect of flowing water has not been incorporated in this context, and Chapter 4 addresses this knowledge gap. The research as described in Chapter 4 demonstrates that pairs of Eurasian minnows (*Phoxinus phoxinus*) actively shoal a higher percentage of time when flow is present and that shoal structure changed from a tandem to a side-by-side arrangement. The switch to a side-by-side configuration under (high) flow has, to this author’s knowledge, only been reported once before, in the startle response of giant danio (*Devario aequipinnatus*) schools (Chicoli et al., 2014). Our results thus support their findings and more importantly, strongly suggest that this adaptation may not be limited to one species. A simplified CFD analysis has shown that it in a side-by-side configuration, neither fish benefits from a reduction in energetic costs in terms of drag, contradicting previous studies (Weihs, 1973, Fish, 1999). Despite the simplicity of CFD approach, there is support for our findings, as a recent study that modelled detailed swimming kinematics of mullet (*Chelon labrosus*) schools in various configurations shows that for the lateral distances observed in minnows swimming in a side-by-side configuration (~ 0.5 BL), efficiency is less than that of a single fish (Hemelrijk et al., 2014). Similar results are obtained for the propulsive performance of side-by-side hydrofoils (Dewey et al., 2014). For the minnows, a convincing argument could be obtained by performing detailed simulations that include the fish's swimming motion and fin movements, as these are both used for propulsive movements (thrust) and cost the fish considerable energy depending on the environment (Lauder and Tytell, 2005). Alternatively, a direct comparison in terms of Tail Beat Frequency of each fish in both shoal configurations can provide direct results on energetics. Such approaches have been used for different species to assess the efficiency of shoaling (e.g. Svendsen et al., 2003, Johansen et al., 2010, Killen et al., 2011) and could be part of further analysis.

In Chapter 4 we arrive at a different explanation for shoaling: fish shoal to optimise information transfer, rather than exploiting energetic benefits. Velocity correlations were generally higher under flow than under to standing water, suggesting more efficient communication between fish, and turning correlations were highest when in the side-by-side arrangement. The addition of flow apparently compromises the trailing fish's ability to react to the leading fish using the lateral line adequately (Chicoli et al., 2014), similar to when cut lateral lines lead to fish orienting themselves between others under standing water (Partridge and Pitcher, 1980). Having a neighbour alongside rather than behind, means that vision can be employed (as opposed to the neighbour being in the blind spot) to counter the lack of information available through the lateral line, it being compromised by the properties of the flow. The results presented in Chapter 4, namely that the properties of the flow affect lateral line functioning, and induce an adaptive response of the fish to optimise information transfer through vision, support earlier findings in a different context (Chicoli et al., 2014), and encourages further research into collective behaviour in response to flow. In particular, the relative role of other factors that might induce a side-by-side configuration, such as an demand for food (Krause, 1993b), which presumably would increase in a more costly environment.

In the experiment described in Chapter 4, the simplest possible shoal, consisting of only two individuals (Delcourt and Poncin, 2012) was used as this limits the amount of sources of social information for an individual to just one. There is evidence that pairwise interactions are essential and persist in shoal sizes bigger than two(Herbert-Read et al., 2011, Katz et al., 2011, Ashraf et al., 2016). For instance, Katz et al. (2011) demonstrated that in standing water, the pair-wise interactions (in terms of matching swimming speed) of golden shiner (*Notemigonus crysoleucas*) persist in shoals up to 30 individuals. Although our experiment allowed for the most basic interaction rules to be captured, *in situ* minnow shoals commonly consist of many individuals (Garner, 1997, Kottelat and Freyhof, 2007). It would therefore be interesting to investigate if the results of Chapter 4 hold for larger shoals. In recognition of this, we are currently analysing three-fish interactions between minnows under the same experimental conditions as those reported in Chapter 4, but this is not part of this thesis.

The literature review (Chapter 2) reveals that that research assessing the performance of screening systems has been biased towards threatened or economically important species and that there is a demand for the provision of suitable fish screens for multiple species and life stages, including shoaling fish

(Katopodis and Williams, 2012). Selecting species that are representative for different guilds or body morphologies may reduce the need to assess screen performance for every species present (Kemp, 2016). In recognition of this, chub and barbel were selected for as the species of consideration in the experiments described in Chapter 5 and 6. These species differ in morphology and are considered potamodromous (Kottelat and Freyhof, 2007), thus prone to encounter anthropogenic barriers during their life cycle. Both species have been a subject in the context of upstream passage (e.g. Horky et al., 2007, Benitez et al., 2015), and the screening studies presented here will aid in the protection of both species during downstream movements. As chub and barbel are also popular for recreational fisheries in the UK (e.g. Britton and Pegg, 2011), successful techniques for conservation are required.

Many different types of physical screens have been developed (see Chapter 2). According to Environmental Agency guidelines, 10 mm bar racks are deemed appropriate for installation at intakes with Kaplan or Francis turbines to protect eels and smolts (EA, 2009). The experiment described in Chapter 5 is to this author’s knowledge, the first study to empirically compare the fish guiding performance of 30°/45° angled, 10 mm bar racks with either horizontally and vertically oriented bars. According to Horsfield and Turnpenny (2011) and Ebel et al. (2015) the usage of horizontal bars facilitates bar cleaning but from a fish guidance point of view, the same target species can be diverted with a higher bar horizontal bar spacing due to the oval body shape of most fish, while it also allows for better body movements when impinged. In Chapter 5, it was evident that such angled bar racks did not perform very well for guiding chub and barbel, regardless of bar orientation. There were no consistent differences between horizontally and vertically oriented racks, and considering the numbers of entrained fish under both configurations, it would not be justified to conclude one of them is better. Guidance efficiencies were 21.3% and 24.8% across chub and barbel treatments respectively, and these values are likely unsustainably low. Being the proportion of fish that entered the bypass of those that approached/ attempted, guidance efficiency quantitatively takes into account fish behaviour in terms of rejections or avoidance (Vowles et al., 2015, Kerr et al., 2015). By definition, the number of passed fish cannot exceed the number approached, and the reported low values must reflect several possible issues: (1) fish rejected the screen and needed multiple approaches before passage occurred; (2) fish did not approach the screen at all, or (3) fish passed through the screen rather than the bypass. Results presented in Chapter 5 support each of the above. Both species rejected bar racks multiple times (Table 5.4); a high percentage of released fish did not approach the bar racks within the allotted 1 hr (Table 5.2); and entrainment was generally high under each treatment (Table 5.2). This raises important questions for future research (but actually applies to screening research in general): Why do fish of both species reject the bar racks so often instead of venturing along them? Why are the fish reluctant to move downstream? And how can entrainment be prevented/ reduced?

The benthic nature and adaptation to living on the bottom of rivers (Britton and Pegg, 2011) are a first indication as to why barbel, as opposed to chub, remained upstream often and/ or were capable of holding position close to the screen without further movement. But in general, juvenile life stages are under developed and abiotic factors strongly affect their spatial distribution and movement pattern (Pavlov et al., 2008). The commonly observed active- passive movement pattern where fish orient upstream and move downstream tail first (Pavlov et al., 2010) indeed suggests that fish were carefully venturing downstream to the screens. As it is well known that the presence of a screen changes local hydrodynamic conditions (e.g. Raynal et al., 2013a, 2013b), it is reasonable to assume that the bar racks under the tested conditions induced avoidance in chub and barbel.

A coarse assessment of the flow field close to the bar rack under each treatment revealed that a suitable sweeping flow along the racks towards the bypass was not established. Instead, the mean flow was mainly directed through the rack, regardless of bar orientation. Despite sufficiently low escape velocities (<25 cm s^{-1}) present perpendicular to each rack configuration, fish of both species followed the main flow, which resulted in high levels of entrainment. Improving the flow field in front of the bar racks, i.e. reducing the flow through them while maintaining a sufficiently low escape velocity could help minimise entrainment, and increase the efficiency of the bar racks. In turn, that will provide a clearer answer to the hypothesis that horizontal bar racks perform better than traditional vertical ones. Since previous experimental work has shown that 10 mm vertical bar racks are efficient in guiding eels when angled 45°, 30° or 15° to the flow (Russon et al., 2010), there might be possibilities to create a situation in which such racks can be efficient for chub and barbel as well.

Due to large variability in abiotic and biotic factors in the experimental setup of fish passage studies, transferability of knowledge and mitigation opportunities for multiple species is difficult to establish (Kemp, 2016). Valuable information can be gained through studies that directly test different species under the same experimental conditions. For instance, Russon and Kemp (2011) compared the behavioural response of eel (*Anguilla anguilla*) and brown trout (*Salmo trutta*) to accelerating flow created at orifice weirs. Their results show that trout react to the velocity gradient by switching orientation, while eels react to the infrastructure itself. In a direct comparison between green and white sturgeon (*Acipenser medirostris* & *A. transmontanus*), Poletto et al. (2014) reports higher frequencies of screen contacts and impingements at 2 mm wedge-wire screens for the former species. Both species showed strong avoidance responses after encountering the racks, but chub rejected and re-approached the racks significantly more often, while avoiding direct contact. Barbel on the other hand, tended to hold station at the racks and often made direct contact with them. As a result, impingement was more common in barbel than in chub (Fig. 5.10). The results confirm that multispecies screening can be complicated and needs to take into account interspecific differences in behaviour (Enders et al., 2009, Williams et al., 2012).

Building on the results of Chapter 5, Chapter 6 reports an experiment that assessed the performance of 6 mm wedge-wire screens for guiding juvenile chub. This experiment was designed to eliminate the possibility for fish to pass through the screen (using a smaller 3 mm bar spacing), and again to explore the hypothesis that the performance of screen with horizontal bar orientation can be higher than that of a vertical one. Wedge-wire has triangular shaped profile bars as opposed to round ones (Chapter 5), and it was hypothesized that this combined with the small bar spacing would induce more pronounced differences between the horizontal and vertical configuration in terms of hydrodynamics. In the UK, the Environmental Agency recommends 6 mm screens for usage in summer months when fry are at risk of being entrained (EA, 2009). In Chapter 6, it was shown that under certain conditions the horizontal screen can indeed perform better than the vertical one. This was the case under the low but not high discharge regime, indicating an interaction between screen type and discharge regime determined guidance efficiency. Flow fields in front of the horizontal and vertical screen were indeed different, velocity gradients towards the bypass being higher under vertical than screens. Wedge-wire consists of triangular shaped bars, which compared to round ones, are less streamlined and block more oncoming flow (Tsikata et al., 2014), and due to the small spacing (3 mm), the large blocking area induced sweeping flows under all treatments while escape velocities remained below 25 cm s^{-1}, in accordance with EA guidelines for coarse fish (EA, 2009).

Guidance efficiencies were still very low, the highest value was 25.3% for the horizontal screen under low discharge, and similar to the values reported in Chapter 5. With over 90% of chub eventually entering the bypass and entrainment impossible due to the small bar spacing, the low values are the direct result of a high number of approaches required before successful passage. Avoidance was thus high: chub rejected the experimental infrastructure often before entering the bypass. This is a two-fold problem: avoidance can occur where the fish first meet the screen as they face local hydrodynamics that can change dramatically, but also close to the bypass entrance where velocity gradients can be high. Avoidance to bypass conditions has been reported for other species as well (e.g. American shad, Kynard and Buerkett, 1997), or in general to acceleration of flow (e.g. for eel and brown trout, Russon and Kemp, 2011). For this reason it is suggested that the velocity gradient into the bypass is gradual and not too high depending on species (Larinier and Travade, 2002). Avoidance to the screens by chub showed the opposite trend compared to the guidance efficiency, i.e. it was lowest under the LH but highest under the HH treatment. Thus, under the LH treatment, the screen and discharge combination induced lowest avoidance and therefore highest guidance efficiency. Again it is shown that both hydrodynamics and fish behaviour are essential in achieving efficient screening methods, and highlight the need for interdisciplinary research on this topic (Rice et al., 2010, Williams et al., 2012).

The focus in Chapter 5 and 6 is on the comparison between different screens in terms of induced flow fields and guidance efficiency, rather than on determining which screen is more effective in terms of reducing head losses (e.g. Raynal et al., 2013b, Katopodis et al., 2005), which is of importance to hydropower operators. Factors that influence the drag (coefficient) of a screen, associated head losses and velocity distribution in front of it include approach velocity ***u*** and blockage area ***A*** due to screen angle/ characteristics (e.g. Alsaffar, 1974, Rajaratnam et al., 2010). The hydrodynamics results of Chapter 5 and 6 are thus limited to the experimental conditions imposed, and the outcome may be different under other settings. To provide a general understanding of the effect that either horizontally or vertically aligned bars have on the velocity distributions in front of the screen, experiments would be required that specifically assess head losses (e.g. using Bernoulli's equation) and drag (e.g. direct measurements using load cells) under a variety of settings, where one or more variables such as discharge or screen angle are kept constant. In addition, in the experimental setups used, it was not possible to explicitly determine whether the observed fish responses were due to the flow field in front of the different screens, or the physical nature of the screens themselves, although it can be assumed that fish detect the flow fields close to the screen with their lateral line before making contact with it (Bleckmann and Zelick, 2009). To distinguish between the way fish specifically respond to the flow field or screens experiments would be required in which the velocity distributions in front of the screen are kept similar under both bar orientations, e.g. through altering the upstream discharge. Under different settings in terms of e.g. screen angle, a general picture of the effect of bar orientation on screen guidance efficiency could then be obtained. However, to test many treatments with shoals of fish and assess avoidance/ guidance efficiency would be difficult/ expensive and possibly unethical as it requires large amounts of fish. Previous studies have therefore investigated head losses and velocity distributions near screens under variable settings so the outcome could be related to fish swimming capabilities rather than using fish in the actual testing (Katopodis et al., 2005, Raynal et al., 2013b). Such an approach could be an appropriate way forward for further investigation of the proposed advantages of horizontal over vertical bars in the used screens. As these are currently stored in the ICER flume facility, they are available for reuse.

Both chub and barbel are gregarious fish species during their juvenile life stages. In mimicking natural conditions as much as possible in our experimental approach, we released small groups of both species at the beginning of each trial. Throughout volitional movements, shoal cohesion turned out to be weak, as fish left and reformed shoals of 2-5 individuals during trials. Group size further diminished as individual fish negotiated the bar racks or wedge-wire screens while others did not. Hence, it can be concluded that in the species we investigated collective behaviour is not a critical factor in downstream movements and successful screen passage. It is well known that fish that are left behind experience longer delay and are thus susceptible to higher risk of predation, entrainment, or passage via unwanted routes (e.g. Coutant and Whitney, 2000, Castro-Santos and Haro, 2003). Apparently, the benefits of grouping do not outweigh these disadvantages.

Significance of my findings for behavioural models

The finding that fish shoal more as flow rate increases (Chapter 4), maintain cohesion through speed regulation and optimise information transfer at the cost of drag reduction provides a good step forward in the understanding of collective behaviour under lotic conditions. The result is of importance to the further development of behavioural models. While such models, in which agents (e.g. fish) move through time and space while responding to coupled hydrodynamic models, are well established (Willis, 2011), interaction rules as found in Chapter 4, will improve their quality and realism. In turn, the consequences thereof in the context of fish passage (Nestler et al., 2008, Goodwin et al., 2014) should be an interesting topic for future research.

Significance of my findings for screen design

Chapters 5 and 6 highlighted the importance of fish behaviour in the performance of screens, in particular the avoidance responses to hydrodynamic conditions encountered near them. Under the tested conditions, horizontal wedge-wire screens certainly may offer good possibilities for coarse fish to overcome barriers when escape velocity thresholds are not exceeded. It was also shown that bar racks were not successful and further research is required to improve this. For benthic species such as barbel, a possibility could be the addition of a bottom overlay (covering the lower part of the screen) to prevent entrainment close to the bottom. Usage of an overlay has been proven to work for American eels (*Anguilla rostrata*) (Amaral et al., 2003), which are similar in their benthic preference during downstream movements. The results of Chapters 5 and 6 will contribute to ongoing research into optimising fish screening systems and will be of importance to policy makers (such as the Environmental Agency) for future activities.

Additional considerations

Where Chapter 4 demonstrates that shoaling time increases from low to high flow, my findings as presented in Chapters 5 and 6 reveal that shoals break up and reform often in the presence of screens and flow fields. There are several possible explanations for the differences. Firstly, the screens can have brought along factors that physically inhibit shoaling, e.g. by the structure itself. Secondly, the hydrodynamics near screens negatively impact on the lateral line information transfer (Chapter 4) and groups break down passively. Thirdly, it can be an effect of the used fish species, individual motivation levels and their origin. Hatchery-reared fish can be different from wild fish in terms of swimming capabilities and fitness, such as found in salmonids (Enders et al., 2004, Pedersen et al., 2008), and could very well have also affected shoaling propensity. A combination of factors is likely and has consequences for the interaction rules in models that describe fish behaviour near barriers and fish passages. The extent to which shoaling behaviour in hatchery-reared fish differs from that observed in wild fish in the context of fish screening is recommended for further research.

The breaking off of fish from shoals and subsequent passage of smaller shoals or individuals across barriers has been reported in previous studies (Haro et al., 1998, Lemasson et al., 2014). A screen and bypass design that is appropriate to allow the entry of shoals without breaking them up and causing delay for certain members would be more effective and thus emphasizes the need for a better understanding on how shoal integrity is maintained under *changing* flow conditions.

7.1 Future research

The work presented in Chapter 4 encourages further investigation into how different hydrodynamic variables shape fish shoals. For instance, in Chapter 4, the level of free stream turbulence (Reynolds number, *Re*) was kept constant between the low and high treatments, but it is known to affect fish swimming (Liao, 2007).

Turbulence can be expressed in different ways, e.g. Turbulent Kinetic Energy and Turbulence Intensity, and it would be worth investigating how these metrics affect shoaling and interaction rules. Future work should further build on the results from Chapter 4 by investigating the response of a wider range of species, life-stages and, as already mentioned, larger shoals to (changing) flow conditions.

Based on findings from Chapter 5 and 6, future experimental research on fish screening should address several issues. Firstly, trials with wild fish are necessary to confirm whether they display the same response as our hatchery-reared fish to the experimental infrastructure. However, the large numbers of fish used in our experiments might not be readily available or sustainable to extract from inland waters, so careful planning is recommended. Secondly, to validate the results, trials will be required to assess the guiding performance of screens for chub and barbel *in situ*. The same considerations with regards to fish numbers apply here. Thirdly, a different approach could be adopted to better investigate shoaling during screen studies, and possibly to relate it to findings in Chapter 4. A good method would be to track individual and group fish movements using computer software (Lemasson et al., 2014). Detailed trajectories can then provide information on shoal structure and quantification of the delay fish experience before entering the bypass using survival analysis (Castro-Santos and Haro, 2003). Finally, delayed availability of 30° bar racks prevented execution of trials with these under low flow, which should be conducted to make a comparison with the trials already conducted under high flow. And as already mentioned, the screens need to be tested under a variety of flow and angle settings to investigate whether sweeping/ escape flows can be enhanced for better guidance. With the above in mind, experiments should continue to focus on improving multispecies screen performance via an interdisciplinary approach, providing both hydraulic and behavioural data, so that generalisation of results across studies can be realised (Rice et al., 2010). In particular, the performance of horizontal screens of different types should be explored for the wider fish community.

7.2 Conclusions

The aim of this thesis was to 'advance scientific knowledge to aid the improvement of downstream fish passage for gregarious fish'. Conclusions to each of the identified objectives to meet this aim are presented here.

In the general introduction (Chapter 1) an initial objective was formulated.

Objective 1: Review current literature to identify research trends, knowledge gaps and opportunities to improve downstream fish passage for gregarious fish species.

A literature review (Chapter 2) showed that the functions of grouping are well understood, but that for fish, the underlying interaction rules have been studied almost exclusively in the absence of flowing water. It was further shown that the guidance efficiency of physical screens is often poorly understood, the evaluation of their efficiency biased towards species of economic importance, and individuals rather than shoals. The fish's behavioural response to hydrodynamics, especially velocity gradients created by screens, is essential for their performance. Research should aim towards developing efficient screens for multiple species and life stages by taking a combined approach that investigates hydrodynamics and associated fish behaviour.

Objective 2: Quantify the behavioural response of shoaling fish to controlled flow conditions.

For the first time aspects of shoaling behaviour (shoaling time and shoal structure) as well as interaction rules were quantified under flowing conditions using pairs of minnows (Chapter 4). Shoaling behaviour is positively affected by flow rate and interactions were governed by speed regulation. Simplified CFD simulations investigated possible energy savings under high flow, but did not find these. From velocity correlation analysis, it was shown that information transfer is an important driver of shoal formation, rather than energetic benefits in terms of drag reduction.

Objective 3: Quantify hydrodynamics associated with different types and configurations of fish screens.

Under two discharge regimes, the flow fields associated with several different types of screens (bar racks and wedge-wire screens) were quantified (Chapters 5 and 6, respectively). Incorporated in these experiments was the recent development of using horizontally rather than vertically oriented bars in them. Experiments conducted were the first to directly compare both configurations in terms of the flow field they induce. Results showed that, under the tested experimental conditions, bar racks did not induce clear changes in sweeping and escape velocities regardless of bar orientation. This was due to the usage of round rather than flat bars, which determined the blockage area. Horizontal and vertical wedge-wire screens on the other hand, had a greater blockage area due to the triangular shape of the profile bars, and induced clearly different flow fields. Horizontal wedge-wire screens induced lower mean flow gradient and sweeping velocity than vertical ones under both discharge regimes.

Objective 4: Quantify the performance of these fish screens for guiding groups of potamodromous fish.

Chapters 5 and 6 are the first to compare the performance of horizontal and vertical bar racks/ wedge-wire screens for juvenile chub (Chapters 5 and 6) and barbel (Chapter 5). To resemble natural conditions, these fish were released as small groups. Bar racks of any configuration were generally not suitable to divert both species, as entrainment was high. In the wedge-wire experiments, where entrainment was not possible due to the size of the fish in relation to the bar spacing, the horizontal screen performed better than the vertical screen under low but not high discharge, despite inducing lowest sweeping velocities towards the bypass.

Objective 5: Determine the behavioural response of these species to screens and associated hydrodynamics in the context of the observed performance.

Both experiments described in Chapters 5 and 6, confirmed the role of fish behaviour to hydrodynamics in the context of fish passage, in particular avoidance responses as previously reported for economically important species. The guidance efficiency of bar racks and wedge-wire screens was unacceptably low because of this avoidance. Despite interspecific differences between chub and barbel, high numbers of both species ended up entrained at bar racks (Chapter 5). Chapter 6 has demonstrated the importance of chub avoidance response to velocity gradients along the screen and resulting performance. Shoals of both species broke up and reformed often, which illustrates that the findings of Chapter 4 do not necessarily hold under different circumstances. The results advanced the understanding of the fish behavioural response to screens and associated hydrodynamics for the species under consideration.

7.3 Contributions to existing knowledge

As a result of this thesis, a number of original contributions to existing knowledge, in particular the field of fish passage, has been made. In this section these contributions and their implications are outlined, as well as their research impact.

Objective 2 (addressed in Chapter 4):

- The interaction rules of fish were quantified in the context of a flow field, which offers possibilities for the improvement of current agent-based models that have mostly neglected a heterogeneous environment. In particular, the findings can aid in Agent Based Models that attempt to predict passage routes of migrating fish in the vicinity of barriers, which feature complex hydrodynamic conditions (e.g. Goodwin et al., 2014).
- It was shown that optimisation of information transfer, rather than adopting a hydrodynamically efficient structure, is likely to be a primary driver behind shoal formation. The results thus contradict the well-known hypothesis that fish shoal to gain energetic benefits.

The results of this study have been presented at two conferences:

- ‘New insights into schooling behaviour in response to flow’ *International Conference on Fish Passage 2015, Groningen, the Netherlands, June 2015.*
- ‘Collective fish behaviour in response to flow’ *Chalkstream Research Conference, Southampton, UK, June 2013.*

A paper based on the results of this chapter is currently under review in *Proceedings of the Royal Society B: biological sciences*.

Objectives 3 to 5 (Chapters 5 and 6).

- The efficiency of horizontal and vertical screens for guidance of chub and barbel was quantified. Efficiency of horizontal screens, although being implemented already, had not been empirically assessed. These studies were the first to do so. They focused on potomodromous fish species that are often neglected in fish screening research. This section of the research was of particular importance to the Environment Agency (UK), and the results will directly impact further water management decisions.
- It was shown that bar racks with 10 mm spacing are not suitable to divert both species of the tested size ≈ 10 cm. Interspecific differences in behaviour were present, but both resulted in high numbers of entrained fish.
- My results have shown that horizontal 6 mm wedge-wire screens, compared to vertical ones, offer a good possibility for effective guidance of juvenile chub, as they induce lower velocity gradients and sweeping velocities towards the bypass.
- Results have demonstrated the existence of clear avoidance response of chub to velocity gradients. This emphasizes the need for creating hydrodynamic conditions that suit this species, which is of high relevance for those working in fish screen research.
- These remarkable results will definitely aid in the development of more successful screens, with a multi-species approach in mind.
- The fate of downstream migrating shoals of fish at screens has not received a lot of attention in the past. Here, it is demonstrated that shoal cohesion for chub and barbel is not strong and that guidance can be successful for certain members, while others remain at or upstream of screens. In

combination with the results on shoaling behaviour (Objective 2) I conclude that a better understanding is required of the hydrodynamic factors that break up or form shoals near screens. This provides an important platform for further research.

Results from Chapter 6 presented in this thesis has been presented at a conference:

- ‘Horizontal and vertical screens: efficacy in guiding fish schools’ *International Conference on Fish Passage 2016, Amherst, MA, United States, June 2016.*

A paper based on the findings of Chapter 6 is in the final stages of preparation for submission in *Ecological Engineering*.

A paper based on the findings of Chapter 5 is planned for submission in the *Journal of Ecohydraulics*.

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