UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING AND THE ENVIRONMENT

Civil, Maritime and Environmental Engineering and Science

Experimental quantification of fish swimming performance and behavioural response to hydraulic stimuli: Application to fish pass design in the UK and China

by

Lynda Rhian Newbold

Thesis for the degree of Doctor of Philosophy

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ABSTRACT

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EXPERIMENTAL QUANTIFICATION OF FISH SWIMMING PERFORMANCE AND BEHAVIOURAL RESPONSE TO HYDRAULIC STIMULI: APPLICATION TO FISH PASS DESIGN IN THE UK AND CHINA

Lynda Rhian Newbold

Loss of habitat connectivity due to anthropogenic structures is among the greatest threats to freshwater fish populations. Re-establishing river connectivity through fish pass facilities can be an effective and cost-efficient method of enhancing local productivity, yet many are unsuccessful. A good understanding of multispecies swimming performance and behavioural response to hydraulic conditions is therefore needed to improve designs. This thesis aimed to improve knowledge in this field for non-salmonid fish species of conservation concern and economic value.

Swimming performance data were collected for juvenile bighead carp (*Hypophthalmichthys nobilis*), a species threatened by anthropogenic barriers in China, using a range of swim chamber and open channel flume methodologies. Burst swimming performance was relatively weak, especially where multiple high velocity areas had to be passed. In addition, the availability of low velocity areas in a section of open channel flume did not improve endurance, and beyond aerobic swimming speeds these velocity refugia were rarely utilised. Management recommendations for fish pass velocities are presented based on this data. To further explore carp behavioural utilisation of low velocity regions, juvenile common carp (*Cyprinus carpio*) swimming performance and behaviour were evaluated under various wall roughness treatments. Fish generally maintained position close to smooth walls and small corrugations, yet often moved further from medium and large corrugations and into areas of higher velocity and lower turbulent kinetic energy. Thus, performance was not enhanced by the larger areas of low velocity created by corrugated walls.

To assess the influence of accelerating flow on European eel (*Anguilla anguilla*) behaviour, a constricted flume created a velocity gradient representative of that found at anthropogenic structures and downstream bypass facilities. Of 138 downstream moving silver eels approaching the constriction, 46% reacted by changing orientation and/or a rapid burst of upstream swimming. Furthermore, 36% rejected the constricted channel and returned upstream, delaying downstream passage. The probability of a rejection was increased by a high abundance of the invasive parasite, *Anguillicoloides crassus.* These findings have potential implications for bypass efficiencies and escapement to sea. Eel swimming performance and behaviour were also evaluated during upstream passage through a culvert. Traditional corner baffles and prototype sloped baffles improved passage success compared to a bare culvert. Although the prototype created higher barrel velocities and turbulence, eel passage success was equal between the two baffle designs. Installation of the sloped baffle is recommended due to high passage efficiency and the potential to reduce the risk of debris accumulation compared to 90° baffles.

The data presented in this thesis enhances our understanding of non-salmonid swimming performance and behaviour, and are used to recommend approaches to fish pass design for European eel and Asian carp.

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DECLARATION OF AUTHORSHIP

I, Lynda Rhian Newbold 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.

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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;
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Signed: ....

Date:..

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Glossary

Abiotic: Non-living components of an ecosystem.

Allele: one of a number of alternative forms of the same gene.

Anadromous: Type of diadromous migration, where fish spawning occurs in freshwater and most growth occurs at sea.

Aquaculture: The farming of aquatic organisms such as fish, shellfish and plants.

Biotic: Living components of an ecosystem.

Body length (*BL*): Measure of fish length, excluding the caudal fin (measured in cm, mm or m, depending on size range within study).

Bypass: An artificial channel designed to provide a route for downstream migrating fish around barriers to migration, predominantly designed to provide a safer alternative to passage through hydropower dam turbines.

Catadromous: Type of diadromous migration, when fish spawning occurs at sea and most growth occurs in freshwater habitats.

Cost of transport (COT): The cost of moving unit mass over unit distance during fish swimming (measured in J km^{-1} kg^{-1}).

Culvert: A structure that allows water to flow under a road, railway or other infrastructure. Typically a pipe or rectangular channel embedded so as to be surrounded by soil, and made from metal, plastic or reinforced concrete.

Diadromous: Fish migrations between marine and freshwater ecosystems for access to spawning and growth habitat.

Ecosystem services: The benefits provided by ecosystems that contribute to human life. This term encompasses the tangible and intangible benefits that humans obtain from ecosystems, including goods such as potable water supply, and services such as navigation.

Elver: Juvenile European eels following the development of pigmentation, generally referring to those entering freshwater and beginning upstream migration.

Entrainment: Fish movement through a physical screen or into an intake or hydropower facility, typically non-volitionally.

Fish pass: An artificial channel, filled with river water from upstream, created to circumvent barriers to fish migrations, thus facilitating fish movement at structures such as dams, weirs and sluices. Fish pass is synonymous with fishway.

Fishway: See fish pass.

Forebay: An artificial pool of water created from a natural river directly upstream of an impoundment.

Fork length (FL): Measure of fish length, from the snout to the middle rays of the caudal fin (measured in cm, mm or m, depending on size range within study).

Glass eel: Term for juvenile European eels when they reach continental waters following oceanic migration from spawning grounds. Eels lack pigmentation at this life stage.

Habitat fragmentation: Alteration of environment resulting in spatial separation of an organism’s habitat into patches from a previous state of connectivity.

Heterozygosity: A measure of genetic diversity; the frequency of heterozygotes (see heterozygous).

Heterozygous: Having two different alleles for a gene on the two homologous chromosomes (one from each parent); the organism is called a heterozygote.

Homozygous: When identical alleles for a gene are present on both homologous chromosomes (one from each parent); the organism is called a homozygote.

Hydraulics: The study of liquids in motion through pipes and channels, synonymous with hydrodynamics.

Hydrodynamics: See hydraulics.

Lentic habitat: Standing freshwater habitat such as lakes and ponds.

Lotic habitat: Running freshwater habitat such as streams and rivers.

Mitigation: Project intended to offset known impacts to an existing resource from a development or activity.

Optimum swimming speed (U_{opt}): The swimming speed at which the cost of transport is lowest (expressed in m s^{-1}).

Parr: Juvenile salmon over a year old, resident in freshwater.

Plunging flow: Occurs following a drop in water head height. Within a fish pass this refers to conditions where the water level in a pool is below the crest of the weir upstream of it.

Potamodromous: Fish migrations that occur entirely within freshwater ecosystems.

Respirometry: Techniques for calculating the rate of an organism’s metabolism. When studying fish this is conducted in a respirometer by measuring the rate of oxygen removal from the water during swimming activity.

Rheotaxis: The behavioural orientation of fish to water currents. Positive rheotaxis refers to fish facing head first into the current and negative rheotaxis to those moving downstream head first.

Semelparous: species that reproduce once during their life cycle.

Shear stress: When two parallel layers of water masses have opposite forces due to their velocities.

Silver eel: European eel life-stage in which physiological, osmoregulatory and reproductory changes occur to prepare for their migration and spawning; silver eels migrate downstream to return to the ocean and travel to the Sargasso Sea where spawning is presumed to occur.

Smolts: Juvenile salmon at the stage of migration downstream to sea, they have undergone adaptations to live in salt water and are more elongated and with darker fins and more silvery colouration than parr.

Streaming flow: A fast moving layer of water. Within a fish pass this refers to a stream of flow moving over the crest of weirs without a change in head height and staying at the surface of intermediate pools.

Swimming ability: The physiological ability of fish to swim at different speeds (in m s^{-1}) and their endurance (minutes or seconds). This is synonymous with swimming capability and refers to how fast fish can swim but is not equivalent to swimming performance.

Swimming performance: The swimming speeds (in m s^{-1}) or endurance (minutes or seconds) fish exhibit in swimming ability tests. This can be due to both physiological ability and behavioural decisions to cease swimming.

Tailrace: The section of river immediately downstream of a dam.

Thigmotactic: Directed response of an organism to maintain contact with a physical surface.

Total length (*TL*): Measure of fish length, from the snout to the tip of the caudal fin (measured in cm, mm or m, depending on size range within study).

Turbulence: Chaotic flow with variation in the velocity magnitude around a time averaged mean.

Velocity barrier: High water velocities that may prevent fish passage by exceeding swimming ability. These are often created at weirs, sluices, culverts and other channel constrictions, as well as experimentally within flumes.

Velocity gradient: The change in water velocity over a given distance (expressed as m s^{-2}).

Vorticity: How fast a region of flow is spinning (expressed in s^{-1})

Water velocity: The rate at which water changes position in a unit of time (expressed in m s^{-1}).

Yellow eel: Referring to European eels during their growth stage, generally sedentary and living in freshwater habitats to feed and mature for between 5 and 20 years prior to silvering.

Chapter 1: Introduction

1.1. Background

Freshwater habitats support a disproportionate share of global biodiversity. Only 0.8% of the earth's surface is freshwater (Gleick, 1996), yet approximately one third of all vertebrates and 9.5% of all animal species are confined there (Dudgeon *et al*., 2006; Balian *et al*., 2008). Iconic mammals such as the Amazon River dolphin (*Inia geoffrensis*, Blainville 1817) and Eurasian otter (*Lutra lutra*, L. 1758), as well as nearly 4,300 amphibian and 12,740 fish species require freshwater habitats (Balian *et al*., 2008; Lévêque *et al*., 2008). About half of the human population also lives within 3 km of a river or lake, and 90% within 10 km (Kummu *et al*., 2011). In addition to the intrinsic value of biodiversity for human quality of life (e.g. Ghilarov, 2000), the ecosystem services provided by freshwater habitats are estimated to be worth US$ 4.93 trillion annually (Costanza *et al*., 1997). These ecosystem services include supporting (e.g. water and nutrient cycling), provisioning (e.g. food, water for domestic consumption and irrigation, energy supply and navigation), regulating (e.g. flood control), and cultural (e.g. recreation, tourism and spiritual enrichment) services (Postel *et al*., 1996; Hansson *et al*., 2005; Millennium Ecosystem Assessment, 2005; Harrison *et al*., 2010). However, freshwater ecosystems are experiencing a greater decline in biodiversity than their terrestrial counterparts (Ricciardi and Rasmussen, 1999; Millennium Ecosystem Assessment, 2005; World Wildlife Fund, 2012). As the human population continues to expand and pressure increases on natural resources, trade-offs between different services are inevitable (Millennium Ecosystem Assessment, 2005; Harrison *et al*., 2010; Brummett *et al*., 2013).

Fish supply over 16% of humans' global annual animal protein intake (FAO, 2014). In 2011 at least 11.5 million tonnes of fish and crustaceans were provided from inland capture fisheries (UNEP, 2010; FAO, 2012). This industry provides employment for approximately 60 million people (largely in less developed countries in Africa and Asia), 55% of whom are women (FAO, 1999; UNEP, 2010). In addition, the 59.9 million tonnes of aquaculture produced fish in 2010 (70% of which was inland) had an estimated farm gate value of US$ 119.4 billion (FAO, 2012). As the local economy grows, the reliance on fish as a food source tends to decline and the value of recreational fisheries increases (Welcomme *et al*., 2010). In the USA, \$25.7 billion was spent in 2011, on equipment, licenses, accommodation, transport, and other freshwater angling related expenses (U.S. Department of the Interior, U.S. Fish and Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau, 2011). Similarly, in the UK 1 million licensed anglers spent £1.16 billion on inland fishing trips and related costs in 2005, supporting over 20,000 industry dependent jobs (Mawle and Peirson, 2009).

Freshwater fish are under threat from fishing pressure (Maitland, 1995; Birstein *et al*., 1997), water pollution (Reynolds *et al*., 2004; Le *at al*., 2010), flow modification (Changming and Shifeng, 2002; Benejam *et al*., 2010), invasive species (Ogutu-Ohwayo, 1990; Pimentel *et al*., 2005), and habitat loss, degradation and fragmentation (Aparicio *et al*., 2000; Morita and Yamamoto, 2002; Fu *et al.*, 2003). Habitat alteration and loss of connectivity due to anthropogenic structures is among the greatest global threats to freshwater fish populations (Dudgeon *et al.*, 2006; Freyhof and Brooks, 2011). Lateral fragmentation from channelization, dykes and levees can prevent or alter the ‘flood pulse’ (Junk *et al*., 1989) by disconnecting rivers, and their fauna, from productive floodplains, wetlands, side-channels, ponds and lakes (Welcomme *et al*., 1979; Bayley, 1991). Dams, weirs, sluices, and culverts can all longitudinally fragment the aquatic environment and decrease the area and complexity of habitat available to fish (Dunham *et al*., 1997; Santucci *et al.*, 2005; Park *et al.*, 2008). Large dams and the associated reservoirs also convert lotic habitat to lentic, and can alter the downstream geomorphology and temperature regime, thus influencing migratory stimuli, life cycles, and community structure (Webb and Walling, 1993; Ward and Stanford, 1995; Magilligan and Nislow, 2005).

1.2. Barriers to fish migration and habitat fragmentation

There are over 50,000 large dams (> 15 m tall or > 3 million m^3 reservoir; World Commission on Dams, 2000) globally (Berga *et al*., 2006; e.g. Plate. 1.1a). Nearly a quarter of these were constructed at least partly as a source of hydroelectricity (International Commission on Large Dams, 2011). Hydropower can form an important component of renewable energy and provide considerable economic benefits to developing countries, but at a cost to other freshwater services. For example, eleven dams are currently planned for construction on the lower Mekong River, which will provide 6 to 8% of the basin’s electricity demand by 2025 and produce revenues to fund infrastructure and social developments in Laos (International Centre for Environmental Management, 2010). Yet the impoundments will negatively impact those relying on the river for food and livelihoods, with an estimated loss in fisheries revenue of US$ 467 million per year (International Centre for Environmental Managements, 2010; Orr *et al*., 2012). In addition to blocking migratory routes, hydropower dams can result in injury or mortality to fish passing through turbines and over spillways, due to strike, rapid pressure changes, cavitation, shear stress, or grinding in narrow gaps between fixed and moving structures (Cada, 2001, Odeh *et al.*, 2002). The construction of large hydroelectric dams is now dominated by rapidly developing countries, notably Brazil, India and China (U.S. Energy Information Administration, 2011). China’s installed hydropower capacity (249 GW), exceeds the next top three countries combined (USA, Canada, and Brazil) (Hennig *et al*., 2013). There were approximately 22,000 large dams in China at the end of the 20th century, compared to just 22 in 1949 (World Commission on Dams, 2000). Development continues at an unprecedented rate to meet government targets of 300 GW capacity by 2020 (REN21, 2010).

There are an estimated 16.7 million artificial impoundments creating reservoirs with a surface area greater than 100 m^2 (Lehner *et al*., 2011) and unrecorded numbers of small weirs and other low head barriers globally. In England and Wales approximately 26,000 structures have been identified as possible barriers to fish movement, including 16,725 weirs, the majority of which have a head height of less than 3 m (Environment Agency, 2010). Low head barriers can form an important component of navigation and flood defence and in recent years small scale (< 10 MW installed capacity) hydropower developments have increased across Europe (Department of Energy and Climate Change, 2010). However, the full influence of low head structures on fish movement has only been recognised relatively recently (Lucas and Frear, 1997; Gibson *et al.*, 2005). They may form full, temporal (i.e. allow passage under some flow conditions), or partial (e.g. allow passage of stronger swimming individuals or life stages) barriers to migration (Kemp and O’Hanley, 2010; Plate. 1.1b and c).

The small diameter, steep slope and smooth substrate of many culverts creates high water velocities with a lack of resting areas, which can impact fish movement, especially during high flows (Pearson *et al.*, 2006; Franklin and Bartels, 2012; MacPherson *et al*., 2012). At low discharge these same homogeneous conditions can result in a low water depth, exposing parts of the gills or fins to air, and reducing swimming efficiency (Webb, 1975). In addition, downstream scouring of the river bed can create a perched outlet impassable to fish species unable to leap (Mueller *et al.*, 2008; Park *et al.*, 2008). The high number of culverts in many areas makes their potential effect on fish populations large. For example, the Washington State Department of Fish and Wildlife (WSDFW) has so far evaluated 3,204 culverts, identifying 941 total and 1,047 partial barriers, that block 3,848 miles of potential salmon habitat (WSDOT, 2012).

Plate 1.1. Full and partial barriers to fish migrations: a) The Pengshui dam under construction on the Wu River, China, which will form a complete barrier to upstream fish movements with no fish pass to be installed; b) culvert on the Cobblers brook, UK, creating a partial (to some species and sizes) and temporal (dependent on river discharge) barrier to up and downstream fish movement due to low water depth; and c) a gauging weir on the River Wey, UK, creating a partial barrier (some individuals, species, or life-stages) to upstream fish passage due to high water velocities.

Anthropogenic barriers to fish migration have numerous implications for fish populations (summarised in Table 1.1.), which may result in genetic changes, reduced abundance and even the extinction of local fish populations or species (Beamish and Northcote, 1989; Penczak *et al.*, 1998; Larinier, 2001). The best known, and often most severe, impacts are for those fish species that must conduct diadromous migrations to complete their life cycle. There are 128 diadromous fish species globally, of which 87 migrate to the ocean to mature and return to spawn in freshwater habitats (anadromous), while 41 have the opposite life cycle (catadromous) (Gross *et al.*, 1988). Barriers to these migrations can prevent adults reaching suitable spawning grounds and therefore reduce productivity or even lead to extinction (McDowall 2006; Limburg and Waldman, 2009). Perhaps the most famous example is from the Columbia River basin in the USA. Here the construction of 60 large and over 1,200 small dams (NRC, 1996) blocked access to many upstream salmon spawning sites and reduced the survival of downstream migrating juveniles (smolts) to less than 20% (Williams *et al.*, 2001). As a result, the anadromous Pacific salmon runs declined to less than 10% of historic levels (Williams *et al.*, 1999) and disappeared from 40% of their Pacific Northwest range (NRC, 1996). Consequently, subsistence and commercial salmon catches were also reduced, with an estimated annual loss of US$ 475.2 million in personal income (The Institute for Fisheries Resources, 1996). Today catches consist predominantly of hatchery reared fish released to enhance the natural stock. The anadromous Chinese sturgeon (*Acipenser sinensis*, Gray 1835) has also experienced a critical decline partly due to new anthropogenic barriers blocking access to spawning grounds (Dudgeon, 1995; Qiao *et al.*, 2006; Qiwei, 2010). The Chinese sturgeon historically migrated 2,500 to 3,300 km along the Yangtze River to reach at least 16 spawning sites. The construction of the first mainstream Yangtze dam (the Gezhouba dam) in 1981 blocked their migration route and restricted spawning to one 3.7 km long area immediately downstream of the dam (Yang *et al.*, 2006). In 2013 no successful wild reproduction was recorded.

Potamodromous migrations are conducted by fish that move between different freshwater habitats for spawning, rearing, feeding and refuge. These can range from a few tens (e.g. barbell and pike in the UK, Lucas and Bately, 1996; Ovidio and Philippart, 2002; Masters *et al.*, 2003), to several thousand kilometres, longitudinally, or between rivers and lakes (e.g. in South America, Quiros and Vidal, 2000; Carolsfield *et* *al*., 2003). Anthropogenic barriers often block these movements just as they do diadromous migrations (Lucas and Frear, 1997; Lucas *et al*., 1999; Godhino and Kynard, 2009). The migrations of over 40 fish species between the Yangtze River, China, and historically connected lakes have been restricted in recent decades due to the construction of sluice gates (Fu *et al*., 2003). The habitat fragmentation caused by river-lake barriers has altered the fish community structure in the lakes (due to a decline in migratory species), restricted gene flow between populations, and contributed to a decline in the Yangtze River fish catch (Chen *et al*., 2004; 2009; Fang *et al*., 2006). The Yangtze (or Dabry's) sturgeon (*Acipenser dabryanus*, Duméril, 1869) is a potamodromous fish endemic to the Yangtze River and was historically widespread in the middle and upper reaches of the basin (Zhuang *et al*., 1997). Following the construction of the Gezhouba dam, the downstream population could not migrate upstream to historic spawning sites and young fish could not access the rich feeding areas in the mid-Yangtze and surrounding lakes (Zhuang *et al*., 1997). The commercially important Yangtze sturgeon is now extinct downstream of the Gezhouba dam and is classified as critically endangered, possibly extinct in the wild, in part due to habitat fragmentation (Qiwei, 2010).

In addition to blocking migratory routes, barriers to fish movement convert a previously continuous river habitat into small fragmented patches. Often fish cannot move upstream of barriers, but can pass downstream (with or without some injury or mortality), thus gene flow is restricted to the downstream direction. Small, isolated populations are affected more by genetic drift and alterations to allele frequency, and reduced heterozygosity is more common than in large populations due to inbreeding (Freeman and Herron, 2004). A greater frequency of homozygotes and expression of deleterious alleles can lead to inbreeding depression (Begon *et al*., 1996). For example, the white spotted charr (*Salvelinus leucomaenis,* Pallas 1814) is common in Hokkaido, Japan, but populations have been fragmented by many dams. The probability of their occurrence upstream of dams is negatively related to habitat size and isolation period (Morita and Yamamoto, 2002). Upstream populations have lower genetic diversity (measured by number of alleles and heterozygosity) than those downstream of dams (Yamamoto *et al*., 2004), and in the Sufu River an isolated population shows dorsal fin deformation due to inbreeding depression (Morita and Yamamoto, 2000). In addition to the genetic impacts of habitat fragmentation, movements to refuge habitat during disturbances such as drought, flood, fire and pollution events may be inhibited and the subsequent recolonisation prevented or delayed (Detenbeck *et al*., 1992; Lucas and Baras, 2001; Dunham *et al*., 2003).

Alongside the negative impacts of anthropogenic barriers to fish movements, benefits are possible where invasive species are excluded from sensitive ecosystems (Jackson and Pringle, 2010). For example, natural or artificial barriers have been used to exclude invasive brook trout (*Salvelinus fontinalis*, Mitchill 1814) and rainbow trout (*Oncorhynchus mykiss*, Walbaum 1792) from some areas of North America, to protect the native and endangered cutthroat trout (*Oncorhynchus clarkia*, Richardson 1836) from hybridisation, competition and predation (Thompson and Rahel, 1998; Kruse *et al*., 2001). In addition, between 1958 and 1999, 61 sea lamprey (*Petromyzon marinus*, L. 1758) barriers were installed or modified in Great Lakes streams in an attempt to reduce their access to spawning habitat (Lavis *et al*., 2003). As lamprey cannot leap, most were low head vertical weirs with an overhanging lip. However, this type of approach risks unintentional blockage of other non-target fish and isolating populations of the native species, therefore trade-offs must be assessed carefully (Peterson *et al*., 2008; Fausch *et al*., 2009; Pratt *et al*., 2009). In Australia, a selective trap for invasive common carp has been installed within some fish passes. The ‘Williams cage’ utilises the natural behaviour of common carp (*Cyprinus carpio*, L. 1758), which tend to leap when trapped, to separate them from native species that do not jump (Stuart *et al*., 2006). Prior to designing any velocity, height or behavioural barrier to invasive fish it is essential to create exclusion criteria based on a good understanding of the swimming ability and behaviour of both the target and the native fish species.

Table 1.1. Potential consequences of full or partial impediment to fish movements at anthropogenic barriers. Split into the effects on fish populations and the consequences of reduced fish stocks on ecosystem services.

Pressure	**Potential consequences**
Fish populations	
Impeded access to upstream habitat	• Lost access to spawning grounds and habitats required for growth and feeding during various life-stages; • Reduced access to refuge habitat inhibiting survival of extreme events; • Reduced ability to recolonise fragmented habitats after extreme events; • Increased population density downstream of barrier; • Reduced fish species richness and loss of migratory species upstream of barrier; • Reduced spread of invasive species.
Injury and mortality	• Reduced survival during dam passage; • Indirect effects on survival after passage due to injury/stress.
Congregation and delay at barriers	• Increased risk of predation, fishing and disease transmission; • Reduction in energy reserves.
Fragmentation of populations	• Gene flow only in downstream direction; • Enhanced susceptibility to genetic drift; • Inbreeding depression; • Altered life cycle.
Ecosystem services	
Reduced biodiversity and abundance of fish	• Loss of sustainable protein supply to local communities; • Loss of trade and income from wild fisheries resources; • Changes to the food chain; • Changes to ecological processes such as nutrient cycling.

Where barriers threated the sustainability of fish populations, large numbers of hatchery reared individuals are often released to supplement the endangered wild stock. However, this management strategy can be risky. Hatchery reared fish often have reduced fitness compared to wild stock due to the artificial tank conditions (Araki *et al.*, 2008). Large scale hatchery releases risk breeding with wild stock, and causing reduced productivity (Reisenbichler and Rubin, 1999; Chilcote, 2003), genetic changes (Ford, 2002), and loss of local adaptations (Utter, 1998) in wild fish. Large dams restricted the habitat of the Rio Grande silvery minnow (*Hybognathus amarus*, Girard 1856) to 5% of its former range within fragmented populations (Bestgen and Platania, 1991) and captive rearing and release began in the early 21st century to boost the population. However, it was found that allelic diversity was lower in captive bred populations, due to the limited number of broodstock selected, risking detrimental effects on the fitness of wild stocks (Osborne *et al*., 2006). Well designed hatchery supplementation schemes do have their place in fisheries conservation (reviewed in Pearsons and Hopley, 1999; Waples, 1999), however, they do not tackle the cause of population decline. Restoring connectivity, either through dam removal or fish pass installation, can directly tackle the source of decline and therefore lead to a more sustainable recovery.

1.3. Mitigation using fish pass facilities

Re-establishing river connectivity can be the most effective and cost-efficient method of enhancing local fish productivity (Roni *et al*., 2002; 2008). As barrier removal is often not feasible, billions of dollars are spent annually in attempts to maintain migratory routes at new and existing anthropogenic barriers through the installation of fish pass facilities. A fish pass is an artificial channel circumventing a barrier, often referred to as a fishway or bypass (overview in Clay, 1995; Marmulla, 2001; Odeh, 2002). In this thesis ‘fish pass’ will be used to refer to all types of facilities designed to provide up and downstream routes around barriers, including baffled culverts, while bypass will be used for downstream migration routes only.

For upstream movement, technical fish passes are the most common and utilise baffles or weirs to decrease the water velocity within an artificial sloping channel. These include: pool and weir types (Plate. 1.2a) which may have orifices or notches within the weirs; vertical slot passes (Plate. 1.2b); and Denil passes and their variants which are formed of baffles on the floor and/or walls of a rectangular channel (Denil, 1909; reviewed in: Larinier, 2002a, Plate. 1.2c). Nature-like fish passes mimic the form and function of a natural river bed, with a low gradient (1 to 5%), and heterogeneity in substrate material, velocity and depth. Rock ramps apply the same techniques, but can be used to either modify part of a weir for fish ascent, or to reduce a structure’s head height by increasing the downstream bed level (Plate. 1.2d). At very large dams, mechanical fish lifts and locks are more likely to be the most cost effective and efficient solution (Clay, 1995). Both operate on an automated cycle of attraction into the lock chamber or lift 'hopper', lifting, upstream release, and lowering/emptying of the chamber.

Similar to technical fish passes, baffles made of wood, plastic, or metal, can be installed in a culvert barrel to reduce water velocities, increase depth, and provide resting areas for fish (e.g. Rajaratnam *et al*., 1988; 1989; Ead *et al*., 2002; Balkham *et al*., 2010; Feurich *et al*., 2011; Fig. 1.1). The most common are weir like structures (Fig. 1a-c), either fully or partially spanning the culvert diameter, and sometimes including a notch (e.g. Rajaratnam and Katopodis, 1990; Morrison *et al*., 2009). These act as a type of pool and weir fish pass under plunging flow conditions, or create bed friction to reduce velocity when baffles are submerged and flow is streaming (Caltrans, 2007). Corrugated metal culverts or the addition of bed substrate can also be used to reduce the mean cross sectional velocity, and increase the area of low velocity near the culvert edge compared to smooth and bare barrels (House *et al.*, 2005; Richmond *et al.*, 2007).

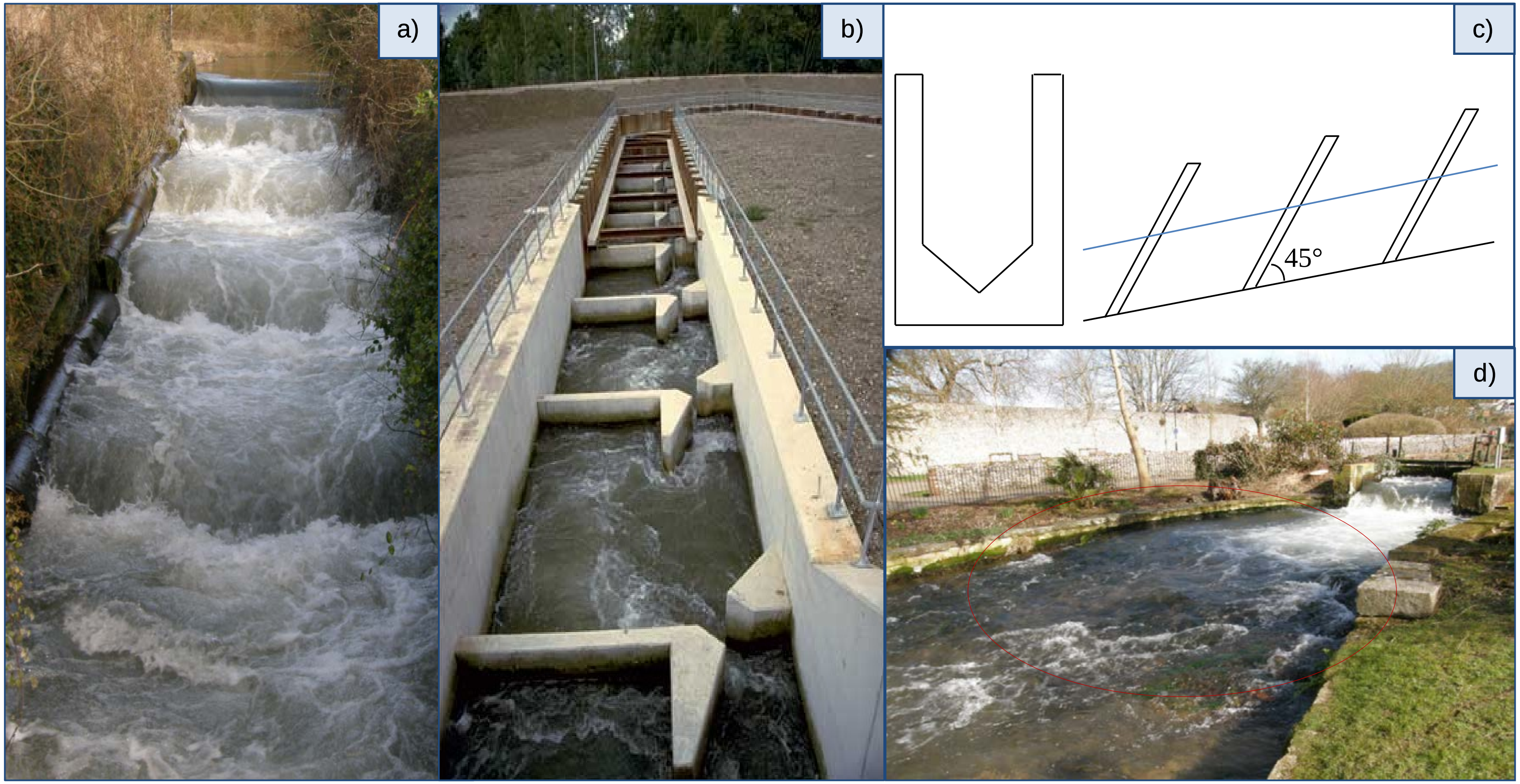


Plate 1.2. Some common fish pass types: a) pool and weir fish pass, which forms a series of steps with lower water velocities within pools for resting, on the River Itchen, Hampshire, UK; b) vertical slot fish pass, designed to allow up and downstream water levels to fluctuate, and for fish to pass at any depth in the water column (Marmulla, 2001); c) front and side view of Denil fish pass baffles, installed within a rectangular channel to create a lower velocity near the channel floor (adapted from Larinier, 2002a); and d) a rock ramp used to reduce the head height of a weir using natural river substrate, River Itchen, Hampshire, UK.

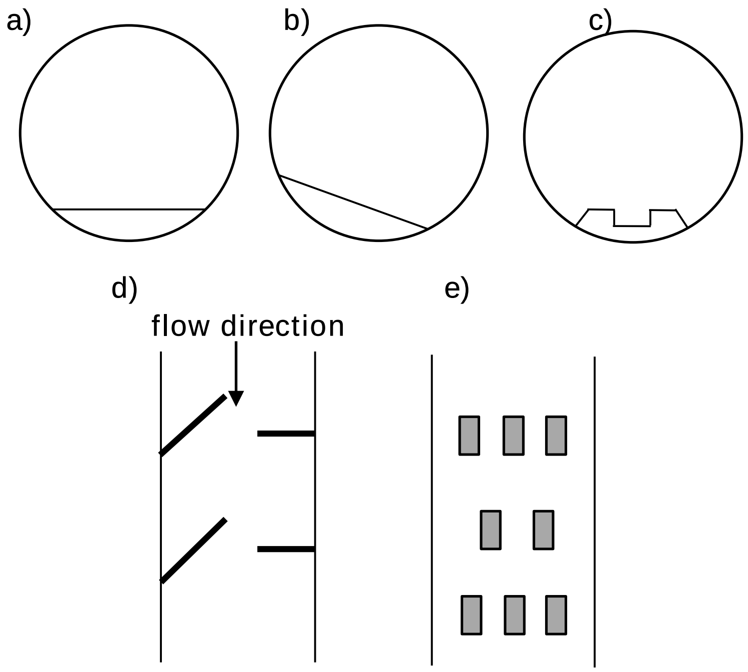


Figure 1.1. Some common types of culvert baffle designs: view as if looking upstream of a) weir baffle, b) corner baffle, and c) Alberta fishway baffle; and plan view of d) offset baffles, and e) small brick shaped spoiler baffles.

The first fish passes in Europe were installed in the mid-18th century (Clay, 1995) and laws were passed in the UK, Ireland, Canada and the USA in the 1880s requiring the provision of upstream passes for some species and on some rivers (historic review in: Katopodis and Williams, 2012). Although the earliest attempts were largely ineffective (Prince, 1914), systematic scientific studies into hydraulic conditions and passage success led to the development in the early 20th century of many designs still in use today (e.g. Denil, 1909; 1938; Clay, 1995). These early pool and weir, vertical slot, and Denil fish passes were designed largely for upstream migrating adult salmonid species, and to a slightly lesser extent clupeids (e.g. shad and alewives) due to their economic and cultural importance in North America and Europe. More recently, nature like fish passes have been constructed and research into solutions for multispecies advanced (Jungwirth, 1996; Marmulla, 2001; Calles and Greenberg, 2005; Katopodis and Williams, 2012).

In many other countries the installation of fish passes is poorly enforced, and designs remain in their infancy. Of 11 large dams planned for the lower Mekong River basin, only three explicitly include fish pass plans, none of which are based on detailed studies of the target fish species (ICEM, 2010). In China, the first fish pass was constructed in 1960, and during the next two decades approximately 100 were installed across the country (Nakamura, 1993). However, when the first dam was constructed on the Yangtze River in 1981 (the Gezhouba dam) artificial stocking was initiated rather than including a fish pass. This approach resulted in less incentive for fish pass installation at new dams upstream and a stagnation in their construction across the country (Nakamura, 1993; Fu *et al.*, 2003; Dudgeon, 2005). The release of new guidance on environmental impact assessment for dams and mitigation methods in 2006 finally caused a revival in Chinese fish passage design, although few have been installed to date.

Downstream bypasses aim to provide a safe passage route around large dams and hydroelectric turbines through a separate pipe or channel. To direct downstream moving fish towards the bypass entrance, a range of physical and behavioural screens have been developed (Clay, 1995; Taft, 2000). Physical bar screens are the most common (Larinier and Travade, 2002), however, maintenance costs are high due to debris accumulation and they can cause injury or mortality to fish through contact with, or impingement on the screen face (Hadderingh and Jager, 2002; Calles *et al.*, 2010). Therefore, behavioural screens have been developed using stimuli such as light, acoustics, bubbles or hydraulics, either alone or in combination, to induce avoidance of the turbine entrance or attraction towards the bypass route (Popper and Carlson, 1998; Larinier and Travade, 1999; Larinier, 2001; Scruton *et al.*, 2002).

The development of downstream bypasses was stimulated by concerns over the survival of migratiing Pacific salmon smolts in the U.S. during the 1940s, much later than the successful installation of upstream fish passes (Katopodis and Williams, 2012). Although many advances have now been made in this area, downstream passage remains neglected for many species. Downstream bypasses are rare at the large number of hydropower dams in tropical countries where fish diversity and abundance is high, including in Thailand, Brazil and China (Quiros, 1989; Marmulla, 2001; Thorncraft *et al.*, 2005; Baigún *et al.*, 2007).

1.4. The effectiveness of fish pass facilities

An ideal fish pass should allow fish to continue up- and downstream migration with no increase in delay, predation or energy expenditure compared to the natural migratory route, and without reducing fitness due to stress, disease or injury (Castro-Santos *et al*., 2009). Evaluation of fish pass effectiveness is largely dependent on determining attraction (e.g. proportion of fish in the dam tailrace that locate the fish pass entrance), entry (proportion of fish approaching that enter), and passage (proportion of those individuals that enter the facility which successfully ascend/descend) efficiencies and delay (Castro-Santos *et al.*, 2009; Bunt *et al.*, 2012).

Many fish passes have been successful in restoring access to habitat and increasing the upstream fish abundance compared to pre-mitigation levels (e.g. Laffaille *et al.*, 2005; Kiffney *et al.*, 2009). However, attraction and passage efficiencies remain highly variable between sites and species, and can range between 0 and 100%, with values less than 50% common (Bunt *et al*., 2012; Noonan *et al*., 2012), despite recommendations to pass 90-100% of diadromous fish (Lucas and Baras, 2001). Studies assessing the effectiveness of culvert retrofits are few, but passage success can vary dependent on species, as well as baffle configuration and dimensions (e.g. MacDonald and Davies, 2007; Franklin and Bartels, 2012). Finally, even if safe ascent or descent is ultimately possible, this may follow a delay between barrier approach and successful passage of several days or weeks (e.g. salmon: Chanseau and Larinier, 2000; eels: Haro *et al.*, 2000a; Winter *et al.*, 2006). Delay can deplete energy reserves (Quin, 2005; Tesch, 2003), result in missing optimal oceanic conditions for survival and growth (Folmar and Dickhoff, 1980; McCormick *et al*., 1998; Stefansson *et al*., 2003), and enhance the risk of predation, fishing mortality and disease transmission where fish congregate (Ruggerone, 1986; Riemen *et al*., 1991; Ward *et al*., 1995; Briand *et al.*, 2003; Makrakis *et al*., 2007; Garcia de Leaniz, 2008). Many semelparous fish cease feeding during their spawning migrations (e.g. adult salmon, Quin, 2005; adult European eel, Tesch, 2003), thus delay can diminish their finite energy stores, decrease fitness, and potentially reduce recruitment (Rand and Hinch, 1998).

The low efficiencies and long delay reported for many existing fish passes highlight an urgent need to improve designs. A number of variables can influence fish pass efficacy, including site specific factors dependent on the barrier and watercourse characteristics (reviewed in: Pavlov; 1989; Clay, 1995; Marmulla, 2001; FAO and DVWK, 2002). However, the hydraulic conditions at the entrance and within a fish pass can have a large impact on passage success (reviewed in: Larinier, 2002b; Castro-Santos and Haro, 2008). Therefore, there is a need to quantify fish swimming ability and behaviour to create favourable hydraulic conditions transferable between location and fish pass type.

As traditional designs were developed predominantly for salmonid species, this thesis aims to advance the understanding of non-salmonid fish swimming performance and behavioural response to hydraulic conditions, to contribute towards improvements in multispecies fish pass designs. Research will focus on fish pass design in China where dams are under construction at an unprecedented rate but fish pass installation is rare, and the UK where numerous low head structures still impede migrations. The literature review presented in Chapter 2 will inform the development of research objectives that concentrate on specific research areas (Chapter 3).

Chapter 2: Review of the current fish swimming ability and behaviour literature and its application to fish pass design

2.1. Introduction

Anthropogenic barriers to migration and habitat fragmentation can reduce fish diversity and abundance, and threaten population sustainability (Lucas and Baras, 2001; Collares-Pereira and Cowx, 2004; Dudgeon *et al.*, 2006). Fish pass facilities are therefore commonly installed at dams worldwide in an attempt to maintain, or restore, river connectivity (Katopodis and Williams, 2012). In addition, culverts are increasingly being designed to accommodate fish movements (e.g. Balkham *et al.*, 2010; Kapitzke, 2010; Barnard *et al.*, 2013).

It has long been recognised that the success of mitigation measures to maintain freshwater connectivity are dependent on a good understanding of fish swimming ability (e.g. Stringham, 1924; Bainbridge, 1960; Collins and Eling, 1960; Brett, 1964). Water velocities exceeding capability will prevent passage, therefore this is the main ecological metric accounted for in fish pass design guidance (e.g. Clay, 1995; FAO and DVWK, 2002). Fish pass and culvert length and slope, the dimensions of pools, slots and orifices, and the frequency of resting pools should all be determined based on the resultant water velocity and the ability of fish to move upstream (Clay, 1995). Likewise, the attraction flow must be strong enough to be detected by fish within the dam tailrace without excluding weak swimming species (Weaver, 1963). At intake screens, the escape velocity (perpendicular to the screen face) must be low enough to allow fish to escape injury or mortality from impingement (Hadderingh and Jager, 2002; Calles *et al.*, 2010) and, at behavioural barriers, velocities should not prevent fish responding to the stimuli (Turnpenny and O’Keeffe, 2005).

Despite a long history of research into fish swimming abilities (Hammer, 1995; Katopodis and Williams, 2012), fish pass attraction and passage efficiencies remain highly variable (Bunt *et al.*, 2012; Noonan *et al.*, 2012). As swimming ability depends on fish species and life stage (Katopodis and Gervais, 2012), a historic bias towards designing fish passes for strong swimming adult salmonidae has been widely blamed for low efficiencies for other species (Petts, 1989; Mallen-Cooper, 2007; Katopodis and Williams, 2012; Foulds and Lucas, 2013). The widespread swim chamber methodologies used to quantify swimming ability have also come under recent criticism. Several studies have shown that data obtained in swim chambers can underestimate swimming ability and result in conservative fish pass velocities, which although not an impediment to passage can reduce attraction to the entrance (Plaut, 2001; Peake, 2004a; Peake and Farrell, 2006; Tudorache *et al.*, 2007; Castro-Santos and Haro, 2006). Furthermore, the trend of basing designs on swimming ability alone has resulted in a historic lack of consideration of fish's behavioural response to the hydraulic conditions experienced, which may prevent, limit, or delay passage (Castro-Santos and Haro, 2008; Enders *et al.*, 2009; Rice *et al.*, 2010; Williams *et al.*, 2012). This chapter reviews the test species and methodologies used in swimming ability studies to date and why fish behaviour is important, to understand how biases in the literature have influenced fish pass facility design and to identify areas requiring further research.

The remainder of this chapter is split into two main sections: section 2.2 provides a narrative review on how swimming ability and behavioural research is applied to fish pass design; and section 2.3 presents a quantitative review to highlight trends and gaps in the swimming performance literature. As this thesis focuses on fish pass design in China and the UK, a Chinese language review is also completed as part of section 2.3.

2.2. Narrative review: The application of fish swimming performance and behavioural data to fish passage design

2.2.1. Fish swimming speeds

Most fish swimming is powered by contraction of the red and white lateral muscle fibres to cause body and caudal fin undulation (Videler, 1993). Red muscle contraction is fuelled by aerobic respiration oxidising fats and carbohydrates for slow speed swimming (Bone, 1978). White muscles are increasingly activated at speeds exceeding the maximum aerobic capacity, and are fuelled by anaerobic glycolysis (Johnston, 1981;

Webb, 1994). Many species also have a layer of pink muscles recruited at intermediate speeds (Johnston *et al.*, 1977; Coughlin *et al.*, 1996).

Fish swimming speeds have been classified into three modes based on the muscles activated and the relationship between speed and endurance: burst, prolonged and sustained swimming (Beamish, 1978; Fig. 2.1). Sustained speeds (also known as continuous or cruising) can be maintained for long periods, primarily using energy derived from aerobic processes to power red muscles (Brett *et al*., 1958), and are used for station holding and routine movements. Water velocities below a fish's maximum sustained speed should be passable regardless of the distance covered, therefore, this is often recommended in long culverts, fish pass pools, and at the approach to screens (Peake *et al.*, 1997a; Turnpenny and O'Keeffe, 2005; Armstrong *et al.*, 2010). For convenience during laboratory tests a time limit of 200 min (recommended by Brett, 1967) is often used in endurance tests, at which it is assumed fish are swimming at sustained speeds. However, 60, 100 and 120 min trials are also common (e.g. Jones *et al.*, 1974; Mesa and Olson, 1993; McDonald *et al*., 1998).

Burst swimming is powered by anaerobic metabolic processes and contraction of white muscle fibres. This high speed swimming can only be maintained for a short time before a rest period is required for glycogen resynthesis and removal of muscle lactate (Smit *et al*., 1971; Wilson and Egginton, 1994). Burst speeds are usually defined as speeds that result in fatigue within 20 seconds (Beamish, 1978). Short duration, high swimming speeds are essential for predator escape, prey capture and passage of short velocity barriers. Passage success at sluices, weirs, and vertical slots or orifices in technical fish passes is often determined by burst swimming ability (Mallen-Cooper, 1994; Russon and Kemp, 2011a; Russon *et al.*, 2011).

Prolonged swimming uses both aerobic and anaerobic processes to power red and white muscle fibres, with an increasing contribution from the latter at higher velocities. Prolonged speeds are commonly classified as those resulting in fatigue between 20 seconds and 200 minutes (Brett, 1964). These intermediate speeds are likely to be regularly used during ascent of fish passes and culverts (Belford and Gould, 1989; Bunt *et al.*, 1999). Swimming at prolonged speeds is also reflected in a gait change for many fish species, whereby as more white muscle fibres are recruited and anaerobic processes must be increased, a transition from steady to unsteady swimming occurs (Peake and Farrell, 2004; Cannas *et al.*, 2006; Svendsen *et al.*, 2010).

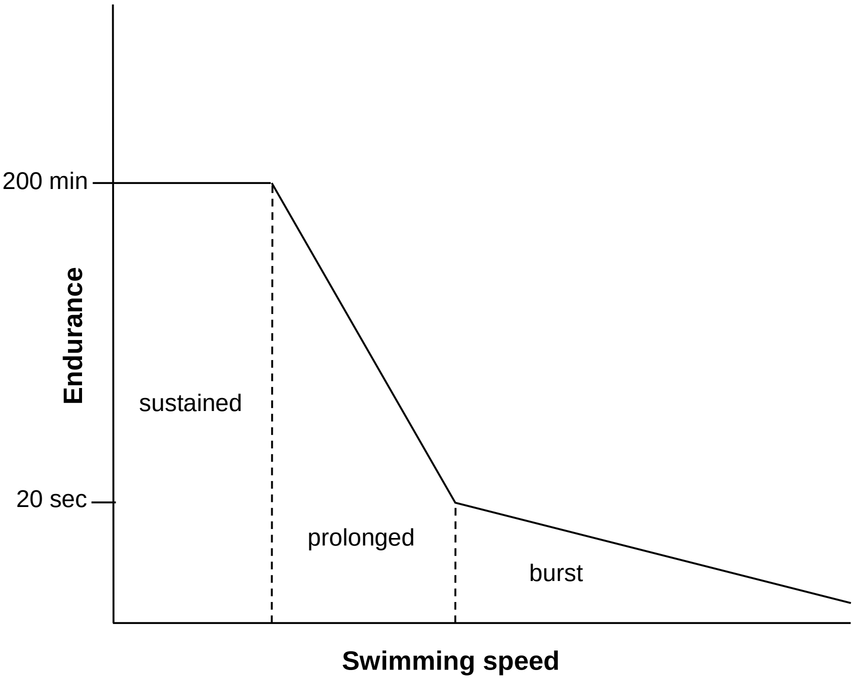


Figure. 2.1. Theoretical relationship between fish swimming speed and endurance, illustrating the three swimming speed categories: sustained (normally classified as > 200 min), prolonged (20 s – 200 min) and burst (< 20 s).

In burst and prolonged modes there is a negative relationship between endurance and swimming speed (Fig 2.1). This association is described by a log-linear relationship within each mode (Brett, 1964):

$$\ln E = a + bU \tag{2.1}$$

where ln$E$ is the natural log of endurance, U the swimming speed (relative to fish length; BL s^{-1}), and a and b regression coefficients that vary dependent on whether fish are swimming in the burst or prolonged mode (Videler, 1993; Castro Santos, 2005).

The endurance limits commonly applied to define swimming modes during performance studies (i.e. burst < 20 s, sustained > 200 min; Fig. 2.1) are somewhat arbitrary values. In reality the transitions do not occur at discrete time intervals and may be variable between species. For example, 200 min is not always a biologically relevant cut off time for assuming a switch from prolonged to sustained swimming speeds (Bernatchez and Dodson, 1985), and for juvenile Atlantic salmon (*Salmo salar*, L. 1758) the switch appeared to occur at 15 to 20 min (Peake *et al.*, 1997a). In addition, Lake sturgeon

(*Acipenser fulvescens,* Rafinesque, 1817) showed apparently no change in the swim speed – endurance slope between prolonged and burst speeds (Peake *et al*., 1997b). In contrast, Castro-Santos *et al*. (2013) recently showed that the burst speeds of brook trout (*Salvelinus fontinalis,* Mitchill 1814) actually fall into two modes, with an additional change in the speed-endurance slope above approximately 18 BL s^{-1}.

As swimming speed increases the energy derived from anaerobic processes increases. Anaerobic mobilisation of energy stores leads to physiological disturbances, which must be reversed following exercise, through increased oxygen consumption (known as post-exercise oxygen consumption; EPOC). The anaerobic cost of swimming can therefore be studied by evaluating EPOC and the time needed for oxygen consumption to return to resting levels (e.g. Peake and Farrell, 2004). This recovery time after fatigue can be 1 or more hours (Lee *et al*., 2003; Reidy *et al*., 1995), therefore, fish swimming endurance at a test velocity can also depend on previous exercise intensity (Jain and Farrell, 2003).

2.2.2. Forced methods to quantify swimming performance

The ‘fish wheel’ (Plate 2.1a) is one of the oldest pieces of apparatus used to study fish swimming performance. It was first employed in the 1940s (Fry and Hart, 1948; Radcliffe, 1950) and later refined by Bainbridge and colleagues in the 1950s (Bainbridge, 1958; Bainbridge and Brown, 1958). Fish are placed in the rim of a large horizontal wheel which is rotated in the opposite direction to movement, whilst keeping the animal stationary relative to the observer. Some of the seminal research linking swimming speeds and endurance, and on the kinematics of swimming (e.g. tail beat frequency and amplitude), were conducted in fish wheels (e.g. Bainbridge, 1958; 1960), although they are less often utilised today.

Due to heterogeneous flow conditions in the fish wheel, swim chambers were designed to provide an enclosed homogeneous test area, which was also suitable for respirometry studies (Blazka *et al*., 1960; Brett, 1964; Plate. 2.1b and c). A motor controls water velocity and drives flow through a rectangular or cylindrical test section. There is no air-water interface and baffles and screens help to create homogeneous flow conditions that are as close to laminar as possible. Therefore, despite occasional accelerations and decelerations, fish swimming speed can be assumed to be on average equal to the water velocity (Nikora *et al*., 2003). To encourage active swimming until fatigue, fish attempting to rest are normally stimulated by electrifying the downstream screen, tapping the chamber, or fluctuating the water velocity (Smit *et al.*, 1971; Mesa and Olson, 1993; Nikora *et al.*, 2003). Since their introduction in the 1960s, studies using swim chambers have dominated the swimming performance literature.

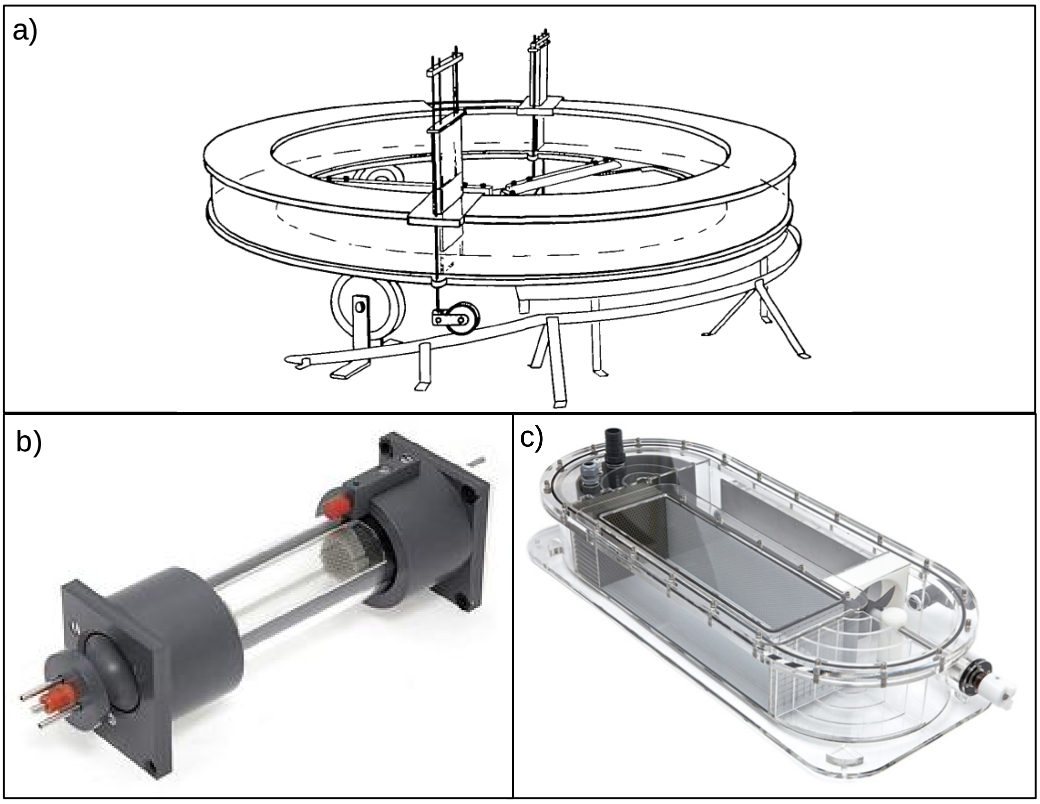


Plate 2.1. Apparatus used to measure fish swimming performance: a) Fish wheel (Bainbridge, 1958); b) Modern Blazka type swim chamber respirometer (Loligo Systems ApS, Denmark); and c) Brett type swim chamber (Loligo Systems). The modern chambers produced by Loligo Systems are adaptations of the early designs used for fish swimming performance and metabolism experiments (Blazka *et al.*, 1960; Brett 1964).

Two protocols introduced in the 1960s have accounted for the majority of swim chamber based swimming performance studies to date, the incremental and fixed velocity tests (reviewed in: Hammer, 1995; Plaut, 2001). The former measures prolonged swimming speeds by incrementally increasing the water velocity at set time intervals, until fish fatigue (Brett, 1964; results reviewed in: Beamish, 1978). The critical velocity (U_{crit}) is then calculated as:

$$U_{\text{crit}} = V + [\Delta V(t/\Delta t)] \tag{2.2}$$

where V is the highest velocity maintained for the entire time interval (cm s^{-1}), ΔV is the velocity increment (cm s^{-1}), t is the time elapsed at the final velocity before fatigue (min) and Δt the time interval used (min).

In fish passage research, the critical swimming speed is often interpreted as the maximum speed fish can maintain for a specific time interval. Assuming the time increments equal the duration of ascent and the U_{crit} equals the swimming speed employed, this equation can be used to define passable velocities (e.g. Jones *et al.*, 1974; Peake *et al.*, 1997a; Mesa *et al.*, 2004). For example, to pass a 100 m culvert in 30 min would require a ground speed of 0.06 m s^{-1}, therefore, assuming a swimming speed equal to the 30 min U_{crit} (e.g. 0.65 m s^{-1}), water velocity in the culvert should not exceed the U_{crit} minus the ground speed (e.g. 0.59 m s^{-1}). By shortening the U_{crit} time intervals, a shorter passage time can be assumed (e.g. to 10 min, Jones *et al.*, 1974). However, this analysis is severely limited by the assumptions that fish will choose to swim at their U_{crit} and that the time required to pass will not exceed the duration selected (Peake, 2004a). By evaluating the volitional swimming speed of smallmouth bass (*Micropterus dolomieu*, Lacepède 1802) during flume ascent, Peake (2004a) demonstrated how culvert criteria based on their U_{crit} (Cooke and Bunt, 2001; Peake, 2004a) would be highly conservative. In reality, the fish's swimming speed was positively related to water velocity (Peake, 2004a).

An alternative application of the U_{crit} assumes that it is equivalent to the fish's maximum aerobic capacity, and that velocities below this should therefore be passable without incurring fatigue (e.g. Mateus *et al.*, 2008; Kieffer *et al.*, 2009). Yet, during the incremental protocol white muscle activation is common at approximately 80% of the U_{crit} (Webb, 1971; Hudson, 1973; Geist *et al*., 2003), and there is often a short period of restless swimming and anaerobic metabolism following each velocity increment (Webb, 1971; Hudson, 1973). Furthermore, the results can depend on the velocity and time increments selected (Farlinger and Beamish, 1977). Therefore, maximum aerobic capacity may not be reliably estimated using this protocol. An alternative approach to determining maximum aerobic swimming ability is the use of electromyogram (EMG) technology to record the velocity at which white muscle recruitment occurs (Wilson and Egginton, 1994; Taylor *et al*., 1996). However, this method is rarely utilised due to cost constraints and the simplicity of the incremental velocity method.

The fixed velocity test evaluates the time to fatigue (i.e. endurance) at a single velocity. By testing fish at a range of velocities, sustained, prolonged and burst swimming speed ranges can be evaluated. Therefore, fixed velocity tests are often utilised to determine water velocities within a target species sustained or burst swimming ability (e.g. Berry and Pimentel, 1985; Langdon and Collins, 2000). Standard protocols do not exist for the increase in velocity from acclimation to test conditions (Hammer, 1995) and no research has examined whether this affects endurance. Methods often report a gradual increase in velocity over 1 min (e.g. Swanson *et al*., 1998), short increments to allow adjustment to intermediate speeds (e.g. Jones *et al*., 1974), a ‘steady; or ‘sudden’ increase, or do not provide details (e.g. Peake and McKinley, 1998; Langdon and Collins, 2000).

Bainbridge (1960) was among the first to recognise the importance of the relationship between fish swimming speed and endurance for predicting the traversable distance, and its application to the design of trawling gear and fish passes (e.g. Peake *et al.*, 1997b; Adams *et al.*, 2000). Maximum distance of ascent ($D_{\max}$) through a velocity barrier can be calculated from the fish’s ground speed (difference between swimming speed [U] and water velocity [V]), and endurance at that speed (E) as:

$$D_{\max} = (U - V) \times E \qquad (2.3)$$

Or based on equation 2.1:

$$D_{\max} = (U - V) \times e^{a+bU} \qquad (2.4)$$

No headway can be made until swimming speed exceeds water velocity, beyond which there is a positive relationship between swimming speed and distance of ascent, up to an optimum (Fig. 2.2). At speeds faster than the optimum, fatigue will occur too quickly to maximise distance. The ‘distance maximising speed’ is equal to a constant optimum ground speed regardless of water velocity for fish swimming in the prolonged mode and a second faster constant ground speed when swimming in the burst mode. This optimum ground speed is equal to the negative inverse of the slope in equation 2.1 (Castro-Santos, 2005). During predictions of traversable distance it is often assumed that fish will utilise the optimum swimming speed. However, there is large variability in the extent to which species and individuals select for this (Castro-Santos, 2005). As distance is therefore determined by both physiological capacity and behavioural decisions, past ascent models based on ability alone are unrealistic (Castro-Santos, 2005; Castro-Santos *et al.*, 2013).

The fixed velocity test measures endurance starting from a resting state. In reality, fish swimming naturally will switch between sustained, prolonged and burst swimming, with cumulative effects on metabolic processes. Between periods of burst swimming a recovery period is needed to repay the metabolic debt through EPOC. At technical fish passes, anaerobic processes may be needed to achieve high swimming speeds at each weir, resulting in a cumulative depletion of the fish’s energy reserves during ascent (Miyoshi *et al*., 2014). Combined with previous high speed swimming downstream of the barrier, this could result in failure to ascend a fish pass (Burnett *et al*., 2014a). Reduced energy reserves, high lactate levels, and long recovery times following successive periods of anaerobic swimming could even cause delayed mortality in upstream migrating fish (Burnett *et al*., 2014b). This is an area rarely considered in fish pass evaluations (Roscoe and Hinch, 2010), or in swimming performance studies.

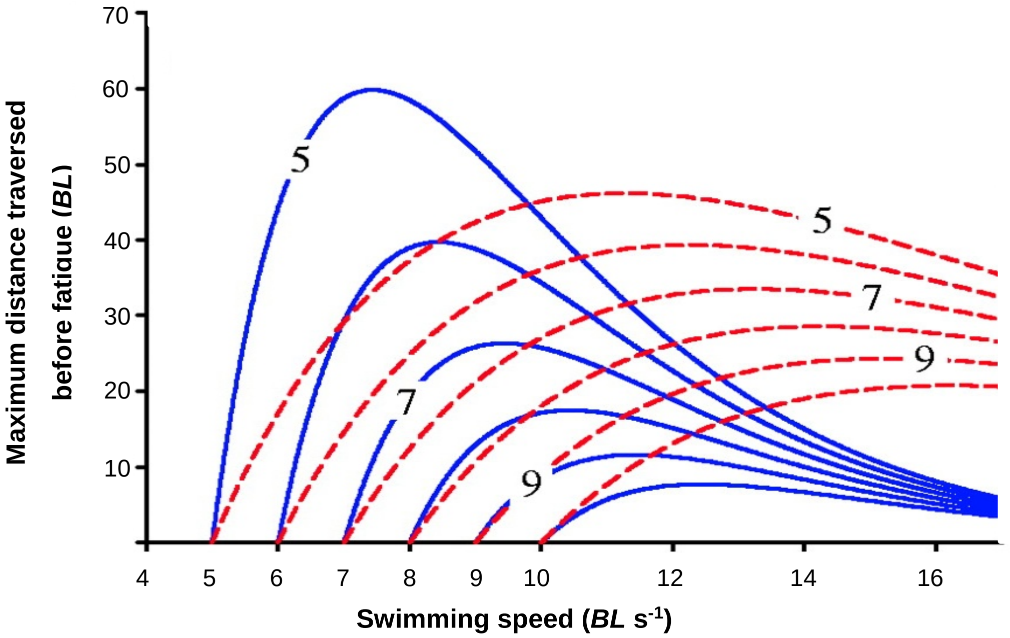


Figure 2.2. The relationship between maximum distance of ascent prior to fatigue and fish swimming speed in prolonged (blue) and burst (red) modes, for different flow velocities measured in *BL* s^{-1} (contours) (adapted from Castro-Santos, 2005).

Alternative methods for quantifying anaerobic swimming performance are the sprint and constant acceleration (U_{max}) tests. The latter is similar to the U_{crit} test but employing time intervals of 1 min or less to reach higher swimming speeds (Farrell, 2008). Burst and sprint swimming are occasionally used interchangeably, but the latter usually refers to very high speeds maintainable for only 1 or 2 seconds (Domenici and Blake, 1997; Nelson *et al*., 2002), which is the convention followed in this thesis. To evaluate the highest sprint speeds a startle response can be initiated (Domenici and Blake, 1997) through electric shocking (Lyon *et al*., 2008), release of a weighted object from above (Tudorache *et al.*, 2008), grasping the caudal fin (Peake *et al*., 2000), or squirting a jet of water at the fish's body (Mueller *et al*., 2006). The U_{max} and sprint methods have had less direct application to fish passage design, therefore are not discussed further here.

Alongside the early empirical research in fish swimming performance, a theoretical approach to predicting maximum swimming speed was developed. This applies the relationships between fish swimming speed, tailbeat frequency, amplitude, and stride length (distance moved in one left-right-left tail beat cycle) explored in early swim chamber research (Bainbridge, 1958; Wardle, 1975; Zhou, 1982). The speed of muscle contraction determines the tailbeat frequency, which is linearly related to swimming speed at all but the slowest velocities (Bainbridge, 1958; Smit *et* al., 1971; Hudson, 1973). Therefore, the maximum swimming speed is theoretically predictable from the speed of muscle contraction (Wardle, 1975).

Zhou (1982) studied white muscle contraction times for six fish species at various temperatures and body length and also explored the influence of oxygen consumption rate and glycogen stores on endurance. He used this research to predict maximum swimming speeds and endurance at anaerobic speeds. Beach (1984) then applied Wardle's (1975) research on maximum swimming speeds and Zhou's (1982) work on muscle contraction times and endurance, to model the relationships between maximum swimming speed, endurance, body length and temperature: there is a negative relationship between speed and endurance, but larger fish have a faster maximum swimming speed due to increased stride length, and longer endurance due to greater oxygen consumption rates and glycogen stores (Brett, 1965; 1972); high temperatures increase maximum swimming speeds due to faster muscle contraction, but this causes a faster depletion of glycogen and therefore a reduction in endurance (Zhou, 1982). Despite the recognition that fish will not necessarily swim at maximum speeds, the graphs produced by Beach (1984) graphs have since been replicated in several fish pass design guidance documents across North America and Europe (e.g. Bell, 1991; Clay, 1995; Larinier, 2002b; Armstrong *et al.*, 2010). These theoretical endurance curves also unrealistically assume that fish will swim to complete exhaustion, glycogen stores are constant between individuals, red and white muscles composition is equal between species, and there is no inter or intraspecific variation in maximum tailbeat frequency or stride length (reviewed in: Castro-Santos and Haro, 2006).

2.2.3. Volitional swimming performance

Alongside the early swim chamber studies of fish swimming performance in the 1960s were a series of flume based experiments using naturally migrating Pacific salmonids (*Oncorhynchus* sp.) and American shad (*Alosa sapidissima*, Wilson 1811). Fish were diverted from the Columbia River through a large open channel flume at Bonneville dam. Swimming ability was evaluated through distance of ascent against various flume velocities and successful ascent of model fish passes (Collins and Elling, 1960; Collins *et al*., 1962; Weaver, 1963; 1965). Behaviour was also evaluated using channel choice experiments and by testing the influence of streaming and plunging flow on passage success (Collins and Elling, 1960; Weaver, 1965).

Although the incremental and fixed velocity swim chamber protocols introduced in the 1960s have since been heavily replicated, the early volitional open channel flume studies were largely forgotten until a recent resurgence (reviewed in: Castro-Santos and Haro, 2006). The recent studies using open channel flumes (as in Plate 2.2) have included assessment of maximum distance of ascent (Colavecchia *et al*., 1998; Haro *et al*., 2004; Castro-Santos, 2005) and the passage of velocity barriers created by experimental weirs (e.g. Kemp *et al*., 2011) and model fish passes (e.g. Mallen-Cooper, 1994). Data are still largely collected through video analysis, but technological advancements have contributed to a number of automated methods, including the use of laser beams, Passive Integrated Transponder (PIT) tags and radio telemetry to evaluate swimming speed and distance moved (e.g. Colavecchia *et al*., 1998; Nelson *et al*., 2002; Haro *et al.*, 2004; Castro-Santos, 2004;).

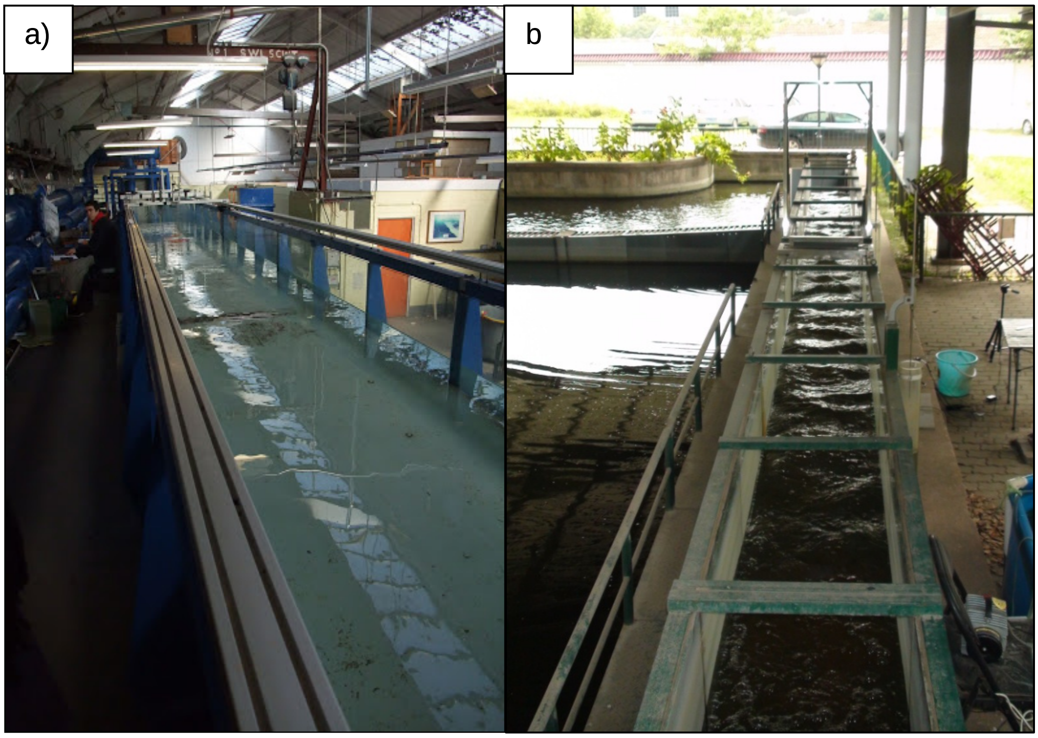


Plate 2.2. Examples of open channel flume facilities used for volitional swimming performance research at: a) the International Centre for Ecohydraulics Research, University of Southampton, UK; and b) the Institute of Hydroecology, Ministry of Water Resources, Wuhan, China.

A number of studies have reported higher fish swimming speeds in large open channel flumes than previously believed possible from incremental and fixed velocity swim chamber tests (Mallen-Cooper, 1994; Peake and Farrell, 2004; Peake, 2008; Holthe *et al*., 2009; Russon and Kemp, 2011a; Castro-Santos *et al.*, 2013). For example, European minnow (*Phoxinus phoxinus*, L. 1758) have a reported 5 minute U_{crit} of 0.16 m s^{-1}, yet individuals of the same size can swim at 0.34 m s^{-1} for at least 24 min in a 4.2 m long flume (Holthe *et al.*, 2009). Equally, Northern pike (*Esox Lucius*, L. 1758) can ascend a 50 m flume against velocities of 1.2 m s^{-1} (Peake, 2008), despite previous swim chamber based research predicting that flow through a 50 m culvert should remain between 0.2 and 0.5 m s^{-1} to ensure successful ascent (Jones *et al*., 1974). Concern has therefore been expressed in the last 15 years over the accuracy of fish swimming ability data collected from swim chamber trials (Plaut, 2001; Castro-Santos and Haro, 2008).

It is believed that the low swimming speeds reached in swim chambers are due to the confined conditions preventing natural performance enhancing behaviours (Peake and Farrell, 2006; Tudorache *et al.*, 2007). At the upper end of the prolonged swimming speed range many species will naturally employ an unsteady burst-and-coast swimming gait. This gait is characterised by two or three large amplitude tail beats followed by fin retraction and a passive, rigid coasting phase (e.g. Peake and Farrell, 2006; Tudorache *et al.*, 2007; Wu *et al*., 2007), which conserves energy by reducing muscle activity and decreasing drag during the coast (Rome *et al*., 1990; Wu *et al*., 2007; Chung, 2009). For example, koi carp (variety of common carp; *Cyprinus carpio*, L. 1758) using a burst-and-coast gait save an estimated 45% of energy compared to steady swimming at the same mean velocity (Wu *et al*., 2007). Under natural conditions the burst is initiated before downstream displacement occurs (Müller *et al.*, 2000); whilst confined in a swim chamber, fish must drift downstream during the coast before a burst of upstream movement (Peake and Farrell, 2006).

As the cessation of swimming in chambers is often associated with a switch from steady to unsteady swimming, it is hypothesised that 'fatigue' is a behavioural response to the unnatural behaviour induced rather than physiological exhaustion (Swanson *et al.,* 1998; Young *et al.,* 2004; Peake and Farrell, 2006; Tudorache *et al.*, 2010). A longer test area allows fish to utilise less constrained burst and coast swimming and reach higher fatigue velocities (Peake and Farrell, 2006; Tudorache *et al.*, 2007). For example, the U_{crit} of juvenile common carp was approximately 27% higher in a 3 m long chamber compared to a 0.87 m one (mean fish length = 262 mm; Tudorache *et al.*, 2007). Likewise, the juvenile shortnose sturgeon (*Acipenser brevirostrum*, Lesueur, 1811) U_{crit} was approximately 26% higher in a 2 m compared to a 1 m chamber (Deslauriers and Kieffer, 2011).

In addition to more realistic estimates of maximum swimming speeds than achievable in swim chambers, large open channel flumes can facilitate a combined evaluation of swimming performance and behaviour. If swimming ability alone determined passage of a velocity barrier, success would be greatest under the lowest velocity treatment, yet this is often not true (e.g. White and Mefford, 2002; Castro-Santos, 2004; Cheong *et al.*, 2006). Fish must also be willing and motivated to attempt passage, which can be influenced by factors including physiological condition, olfactory cues, and behavioural response to flow velocity (Castro-Santos, 2004; Castro-Santos *et al.*, 2013). Over short distances the passage success of walleye (*Sander vitreus*, Mitchill 1811) and white sucker (*Catostomus commersoni*, Lacepède 1803) was higher during 3 and 4 m s^{-1} velocity treatments than 2 m s^{-1}, due to an increased attempt rate at higher velocities; passage success was only improved by lower velocity over distances greater than 4 to 6 m (Castro-Santos, 2004). Shovelnose sturgeon (*Scaphirhynchus platorynchus*, Rafinesque 1820) were also most likely to ascend a flume at velocities of 0.6 to 0.9 m s^{-1}; at velocities less than 0.6 m s^{-1} attraction was poor and above 0.9 m s^{-1} swimming ability was exceeded (White and Mefford, 2002). This type of research will be essential to optimising the flow conditions for fish pass attraction and passage but is currently in its infancy.

The ability to perform short bursts of high speed swimming (e.g. through sluices, vertical slots, notches and orifices) can determine ascent of technical fish passes, rather than endurance over longer distances (Alexandre *et al.*, 2013). Open channel flumes are ideally suited to evaluating burst swimming at short velocity barriers created by flow constrictions. Either a single barrier (e.g. Russon and Kemp, 2011a) or a model fish pass consisting of several high velocity areas and intermediate pools (e.g. Mallen-Cooper, 1992; 1994) can be installed, and passable velocities applied directly to fish pass criteria.

Model fish passes provide the ability to control and manipulate hydraulic conditions, impossible in the field. In addition to evaluating swimming performance by altering velocity, they can be used to test fish passage and behaviour under various designs (Monk *et al.*, 1989; Guiny *et al.*, 2005; Silva *et al.*, 2009). This type of research has confirmed the preference of substrate oriented fish, including Iberian barbel (*Luciobarbus comizo*, Steindachner 1864), eel and lamprey species for submerged orifices and undershot weirs rather than passage routes at the water surface (Silva *et al.*, 2009; Keefer *et al*., 2010; Russon and Kemp, 2011a; Kemp *et al.*, 2011). Although the hydraulic conditions created in experimental fish passes are as realistic as possible, most are scale models. This scaling effect can result in simplified flow conditions, therefore the resting areas and passage routes utilised within a flume may not extrapolate to full scale installations *in situ* (Guiny *et al.*, 2005; Silva *et al.*, 2009). Furthermore, only a short section of fish pass can be installed, which induces unequal flow conditions at each pool (Rajaratnam *et al.*, 1986; Mallen-Cooper, 1992), and limits the need for fish to sustain multiple high speed bursts. It is therefore recommended to validate laboratory findings in the field, before implementing solutions (e.g. Keefer *et al*., 2010).

Despite the benefits of volitional open channel research compared to swim chamber trials, there remain some constraints. Maximum distance of ascent at lower velocities may be limited by flume length (Castro-Santos, 2005). Although survival analysis techniques employ methods to account for censoring (i.e. a $D_{\max}$ determined by flume length rather than fish performance), the results should still not be extrapolated to velocity barriers much longer than the flume within which data were collected (Haro *et al.*, 2004; Castro-Santos, 2006). Distance of ascent and passage success can also be influenced by the fish's motivation to explore upstream regardless of hydraulic conditions. For example, Northern pike, walleye and white sucker were more likely to enter a flume from a small entry tank than a larger one (Peake, 2008). Rio Grande silvery minnow (*Hybognathus amarus*, Girard 1856) moved slower and were less likely to completely ascend a flume filled with cobble or gravel substrate than with sand. Their behaviour was believed to be due to more frequent resting on the coarser substrates, rather than physiological ability or hydraulic stimuli (Bestgen *et al.*, 2010).

Currently, swim chamber based estimates of swimming ability still dominate the fish pass guidance literature. For example, the Environment Agency fish pass manual for England and Wales (Armstrong *et al.*, 2010) recommends the use of the SWIMIT model (SWIMIT V 3.3. © Environment Agency, 2005). The model results are based on swim chamber endurance studies and regression analysis (Clough *et al*., 2004). Although it accounts for species and length variability, the maximum velocities may be conservative due to the constrained methods applied to collect the swimming ability data. Similarly, the American culvert design software, FishXing (Furniss *et al.*, 2006), uses swim chamber based swimming speed estimates to determine suitable water velocities, despite recognising the constraints of these methods in the user manual. The higher swimming speeds reported from flume experiments should be incorporated into fish passage design. Furthermore, combined evaluation of behaviour and swimming performance is required to optimise fish pass velocities for both attraction and ascent.

2.2.4. The effect of biotic and abiotic factors on swimming performance and fish passage design

Considerable interspecific variation in swimming ability exists due to factors such as body morphology (Webb, 1986; Ojanguren and Brana, 2003) and locomotor strategies (Breder, 1926; Kieffer *et al*., 1996). Within a species, the greatest influence on individual swimming ability is body length, with larger fish able to reach higher speeds (Bainbridge, 1978). Therefore the species (or guild) and body length (or age class) are now regularly included when setting fish pass velocity criteria. In addition, swimming ability is influenced by environmental factors, including temperature (e.g. Beamish, 1981; Childs and Clarkson, 1996; Myrick and Cech, 2000), oxygen concentration (e.g. Katz *et al*., 1959; Davis *et al*., 1963; Fu *et al*., 2011) and pollutants (e.g. Howard, 1975; Watenpaugh and Betinger, 1985; Shingles *et al*., 2001). For determining fish pass velocity criteria, water temperature at the time of migration is the only environmental variable currently commonly accounted for (e.g. Beach, 1984; FAO and DVWK, 2002; Armstrong *et al*., 2010). Temperature influences fish swimming performance by its effect on metabolic rate (Beamish, 1981; Bernatchez and Dodson, 1985), cardiac performance (Farrell *et al.*, 1996; Farrell, 2007), and muscle contraction speeds (Section 2.2.1). At low temperatures muscle contraction is slow. This reduces sustained aerobic swimming ability due to the need to recruit white muscle fibres at slower speeds (Rome *et al*., 1984; 1985; 1990), and depresses maximum anaerobic speeds due to limiting tail beat frequency (Wardle, 1975).

Swimming performance trials are normally conducted with fish assumed to be in a healthy condition that swim actively until fatigue. It is common practice during swim chamber tests to omit data from fish that do not orientate to the flow or swim actively at low velocities (e.g. Swanson *et al.*, 1998; Myrick and Cech, 2000; Scott and Magoulick, 2008). For example, 18 and 29% of delta smelt (*Hypomesus transpacificus*, McAllister 1963) were excluded from U_{crit} and fixed velocity tests, respectively (Swanson *et al.*, 1998). In addition, when evaluating volitional performance and behaviour, fish that remain at the release location without entering the flume or moving into the area of interest are often excluded from analysis (e.g. Haro *et al.*, 2004; Vowles *et al.*, 2014). During an evaluation of brown trout (*Salmo trutta*, L. 1758) response to accelerating velocity, between 21 and 67% per treatment failed to exit the release tank, therefore were not included in behavioural analysis (Vowles *et al.*, 2014). The inactive individuals in forced and volitional tests are not explored further, and it is unknown whether their ability and behaviour also diffesr in the field and influence passage success.

Even after excluding inactive fish, there remains considerable and repeatable intraspecific variation in swimming performance at equal temperature and body lengths (Kolok, 1992; Kolok and Farrell, 1994; Marras *et al*., 2010). Although unwillingness to swim and cessation of activity may be due to stress from confinement and handling (Swanson *et al.*, 1998), or simply random variation in behaviour, it could also be a response to individual fitness and health. For example parasite loading can impact swimming ability (e.g. Butler and Millemann, 1971; Sprengel and Luchtenberg, 1991; Moles and Heifetz, 1998), recovery from exercise (e.g. Tierney and Farrell, 2004; Wagner *et al*., 2005) and host behaviour (for review see Barber *et al.*, 2000). Sockeye salmon (*Oncorhynchus nerka*, Walbaum 1792) smolts parasitised with *Myxobolus arcticus* (Pugachev and Khokhlov, 1979) had a mean U_{crit} of 2.92 BL s^{-1} compared to 4.37 BL s^{-1} for unparasitised fish (Moles and Heifetz, 1998). Beamish (1978) suggested that accounting for parasite abundance during swimming trials would reduce variability in results and allow better comparison between studies, yet this has not been followed up.

Traditional deterministic models based on the relationship between swimming speed and endurance use average values to produce a binary response for passage success at various water velocities (i.e. pass or failure; Fig. 2.3a). This method could result in only the stronger swimming fish being able to pass velocity barriers. To account for individual variation in swimming performance and behaviour, models have recently been introduced that predict passage success as a percentage of the population (Haro *et al*., 2004; Castro-Santos, 2006; Fig. 2.3b). The most advanced of these used a stochastic model to predict the $D_{\max}$ of 1000 individuals of American shad, whilst accounting for variation in fish size, swimming ability, and the ground speed selected (Castro-Santos, 2006). This research represents a significant move away from traditional passage success models to account for individual variation in ability and behaviour. Management decisions can then be based on the percentage of a population desirable to pass an modelling suitable velocities. However, further work is required to make it suitable for fisheries management, and the effect of turbulent flow remains neglected (Castro-Santos, 2006).

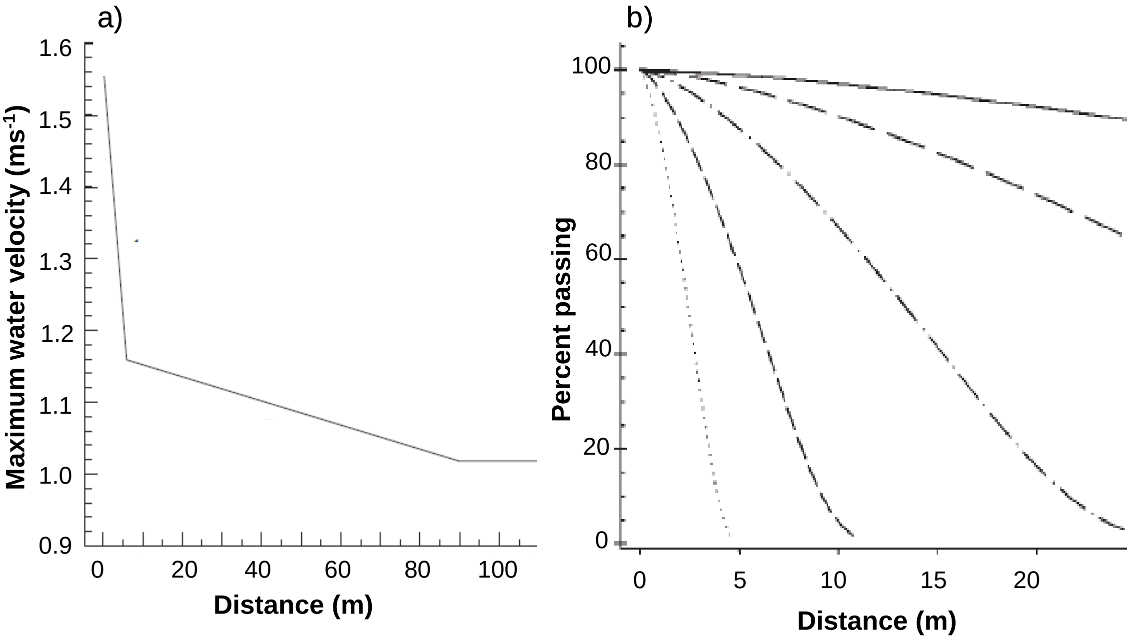


Figure 2.3. The relationship between barrier length and traversable water velocities using: a) a traditional binary model of passage success, where velocities below the line are traversable and those above are a barrier to movement (adapted from Peake *et al.*, 1997a); and b) a stochastic model of the percentage of a population able to pass at water velocities of 1 (solid line), 2 (long dashed), 3 (dash and dot), 4 (short dashed), and 5 (dotted) m s^{-1} (adapted from Haro *et al.*, 2004).

Over the last two decades there has an increase in research into the influence of turbulent flow on fish behaviour, habitat use and swimming performance (reviewed in: Liao, 2007; Lacey *et al.,* 2011; Wilkes *et al.,* 2013). Turbulent flow is characterised by rapid fluctuations in water velocity. Flow fluctuations can destabilise fish, stimulating pectoral fin activation to enhance stability, thus increasing energy expenditure and reducing maximum swimming speeds (Pavlov *et al.*, 2000; Lupandin, 2005; Webb, 2006a; Tritico and Cotel, 2010). Creek chub (*Semotilus atromaculatus*, Mitchill 1818) experienced a 10 to 22% reduction in their U_{crit} in the presence of large cylinders compared to a control condition, due a loss of posture control and displacement (referred to as 'spills'; Tritico and Cotel, 2010). The total swimming costs for juvenile Atlantic salmon at sustained speeds increased between 21 and 31% when the standard deviation of water velocity was increased from 0.05 to 0.08 m s^{-1} (Enders *et al.*, 2005a). Although mean velocity explained 46% of the total variation in swimming costs in this study, the standard deviation accounted for a further 14%.

Despite a negative effect of turbulence on fish swimming performance being common, some studies have found no effect (Nikora *et al.*, 2003) or a positive influence (Liao, 2007). It has long been recognised that shoaling fish can utilise eddies generated by the propulsive movements of conspecifics to reduce their swimming costs (Breder, 1965; Weihs, 1973) and similar behaviours are possible when positioned close to a cylinder or tree branch (Liao, 2007). Under certain flow conditions, D cylinders produce a staggered array of periodically shed vortices, known as a Kármán vortex street. Trout are able to synchronise their body kinematics to slalom between these vortices using a ‘Kármán gait’ and capture energy from eddies (Liao *et al.*, 2003a; b; Cook and Coughlin, 2010; Taguchi and Liao, 2011; Fig. 2.4). The energetic advantage of this behaviour exceeds that of simply swimming in an equivalent reduced velocity area; Kárman gaiting fish consumed 21% less oxygen than individuals swimming in the free stream at a velocity equivalent to the reduced flow downstream of the cylinder (Taguchi and Liao, 2011).

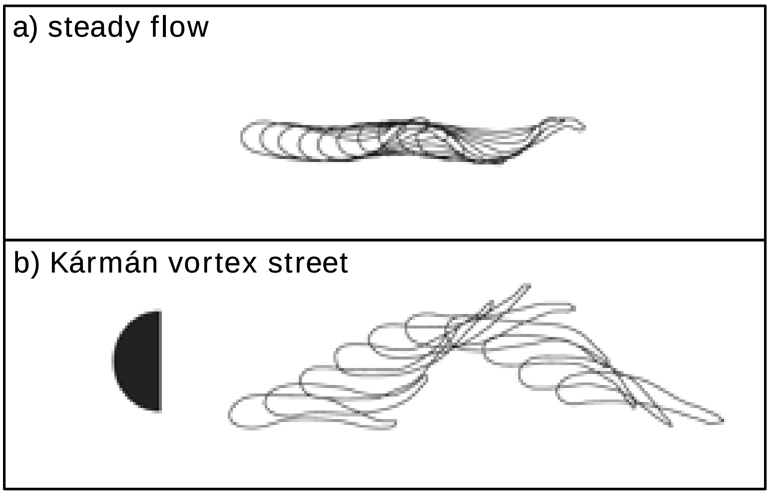


Figure 2.4. Outline of a 10 cm trout swimming in: a) steady flow; and b) a Kármán vortex street created downstream of a 5 cm diameter D shape cylinder. Approximately one tail-beat cycle is shown in 10 body outlines (Liao, 2007).

The influence of turbulence on swimming performance is dependent on the intensity, orientation, scale and periodicity of eddies (reviewed in: Lacey *et al.*, 2011). Although some fish can exploit predictably shed vortices by Kármán gaiting (Liao *et al.*, 2003a; b; 2004; Taguchi and Liao, 2011), turbulence created through unpredictable randomly generated pulsed flows increases the energetic cost of swimming for salmon (Enders *et al.*, 2005a). Turbulent flow only reduced the swimming performance of European perch (*Perca fluviatilis*, L. 1758) when the vortex size exceeded two thirds of fish body length (Lupandin, 2005), and creek chub swimming behind cylinders only experienced spills when eddy diameter was 0.6 to 0.9 times fish total length (Tritico and Cotel, 2010). Eddy diameters much smaller than fish length create evenly distributed moments of force along the body, but as the diameter approaches fish length, torque can destabilise fish and displace them to one side (Webb, 2006a). The orientation of eddies also influences fish stability as their body form and muscle structure result in greater flexibility in the lateral than vertical direction (Webb and Cotel, 2010). Therefore, creek chub had better control of posture and position behind vertical than horizontal cylinders (Tritico and Cotel, 2010). When swimming downstream of the latter, spills began to occur at a lower vorticity, recovery took 25% longer, and fish typically rolled by 90° to enable utilisation of the caudal fin to correct posture (Tritico and Cotel, 2010).

Baffles, weirs and surface roughness in fish passes and culverts reduce water velocity by dissipating energy through the creation of turbulence. Therefore, fish passage may be inhibited even when mean velocity is within the predicted swimming ability of target fish, due to disorientation, destabilisation and downstream displacement (Haro and Kynard, 1997; Silva *et al*., 2012a; Foulds and Lucas, 2013). Swimming performance data from swim chambers are heavily criticised for the uniform microturbulent flow conditions, unrealistic of those within fish pass facilities (Plaut, 2001; Castro-Santos and Haro, 2006). Although open channel flumes have greater flow heterogeneity, variations are still minimised to allow accurate determination of swimming speed, and turbulence is incomparable to fish pass flows (Haro *et al.*, 2004). Therefore, swimming performance during experimental trials using both swim chambers and flumes may exceed that possible in the turbulent flow of technical fish passes.

Fish pass design guidance often includes recommendations for turbulence in terms of the power density (power dissipation per unit volume) (e.g. FAO and DVWK, 2002;

Larinier, 2002c; Armstrong *et al.*, 2010). However, research into the impact of turbulence on swimming performance and behaviour has tended to evaluate the turbulence intensity (Enders *et al.*, 2005a; Lupandin, 2005) or turbulent kinetic energy (TKE) (Nikora *et al.*, 2003; Enders *et al.*, 2005a; Smith *et al*., 2005), with other metrics such as the standard deviation of velocity (Enders *et al.*, 2005a), Reynolds shear stresses (Smith *et al.*, 2005; Silva *et al.*, 2009), eddy diameter (Lupandin, 2005; Smith *et al.*, 2005), and vorticity (Tritico and Cotel, 2010), occasionally included. None of these are considered in fish pass hydraulic recommendations.

There is scope to improve fish pass hydraulic design criteria through research into the turbulence thresholds at which loss of fish's stability and position occur, or energy consumption is significantly increased. Dermisis and Papanicolaou (2009) used this principle and the relationship between fish swimming performance and eddy diameter, to study the likely impact of turbulence on ascent of weirs and fish passes. As well as measuring turbulence intensity, TKE and Reynolds stresses, they evaluated whether the eddy length scale exceeded the average channel catfish (*Ictalurus punctatus,* Rafinesque 1818) body length. It has also been suggested that by identifying an optimum eddy diameter and for minimising the energetic cost of swimming, efficient exercise could be encouraged to increase growth and production in fish culture systems (Webb and Cotel, 2010). With further research the same principle could potentially be applied in fish passes by using cylinders, blocks or hemispheres to generate favourable hydraulic conditions (Silva *et al*., 2012a).

2.2.5. Behavioural response to fish pass hydraulic conditions

Despite the importance of fish swimming ability, understanding this alone will not necessarily ensure fish pass facilities are suitable for target species. The importance of behavioural swimming speed selection and the need to set water velocities that induce attraction as well as passage have already been discussed. This section concentrates on three further hydraulic conditions influencing fish behaviour at passage facilities: velocity gradients, turbulence and flow heterogeneity.

Fish, particularly small individuals, can often exploit small areas of low velocity, commonly referred to as velocity refugia, to save energy and enhance performance against high mid channel velocities. For example, sturgeon in swim chambers commonly utilise a behaviour termed ‘substratum skimming’, whereby they maintain body contact with the floor whilst moving fins for propulsion (Adams *et al.*, 2003). As the U_{crit} is based on mid channel velocity, sturgeon employing this behaviour and utilising lower velocity boundary layers can reach a higher U_{crit} than if they swim actively in mid channel (Adams *et al.*, 1997; 2003; Kieffer *et al.*, 2009; Hoover *et al.*, 2011; Deslauriers and Kieffer, 2012).

Use of low velocity areas may be expected to be of most benefit to weak swimming fish when mid channel velocities are high. Indeed, river lamprey (*Lampetra fluviatilis*, L.1758) approach to an experimental weir along the flume wall, where velocities were lowest, was most common at high discharge (Kemp *et al.*, 2011). The time spent by common dace (*Leuciscus leuciscus*, L.1758), roach (*Rutilus rutilus*, L. 1758) and European chub (*Leuciscus cephalus*, L. 1758) in the corner of an experimental channel was also positively related to mid channel velocity (Garner, 1999). However, chub selected for low velocity areas more often than dace and roach, resulting in an ability to withstand mid-channel velocities approximately 1 BL s^{-1} higher than dace. Furthermore, during volitional ascent of an open channel flume, although white suckers preferentially selected low velocity areas near the wall during the 1.5 and 2.5 m s^{-1} treatments, all species (alewife [*Alosa pseudoharengus*, Wildon 1811], striped bass [*Morone saxatilis*, Walbaum 1792], blueback herring [*Alosa aestivalis*, Mitchill 1814], American shad, walleye, and white sucker swam away from the walls at 3.5 and 4.5 m s^{-1} (Haro *et al.*, 2004).

Small fish have been observed swimming in the low velocity areas of culverts, which is assumed to facilitate passage against high mid-channel velocities (Powers *et al.*, 1997). At present culvert velocity criteria are based on the swimming ability exceeding the mean cross-sectional velocity (Furniss *et al*., 2006). It has therefore been suggested that culvert velocity distributions should be evaluated, to determine if areas within fish swimming ability are available at the edge and to select designs that create the largest areas of low velocity (e.g. Clark *et al.*, 2014; Fig. 2.5). Several experimental and modelling studies have evaluated flow distributions to predict the availability of velocity refugia (Ead *et al*., 2000; Richmond *et al*., 2007; Clark and Kehler, 2011; Clark *et al.*, 2014). Clark and Kehler (2011) modelled isovels in a corrugated metal pipe at different slopes, to calculate the proportion of the cross sectional area where velocity was less than the mean bulk value. To put this research into the context of fish swimming ability, Ead *et al.* (2000) suggest calculating the area of cross section within the prolonged capacity of target fish, while Clark *et al.* (2014) suggest comparing the water velocity distribution with fish velocity and depth preferences. However, experimental research suggests that behavioural utilisation of low velocity areas may depend on the mean channel velocity, species, and life stage (Garner, 1999; Haro *et al.*, 2004), therefore further research is required before this approach is adapted.

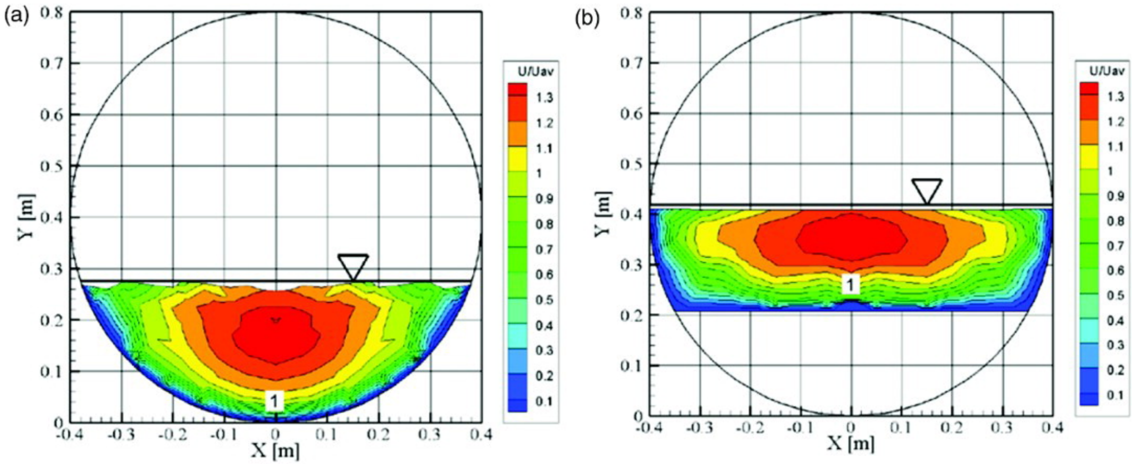


Figure 2.5. Normalised isovels for two culvert designs: a) corrugated metal culvert; and b) corrugated metal culvert with 30% gravel infill, both fitted in a large flume on a slope of 0.27% (Clark *et al.*, 2014). The gravel infill creates a larger area where the velocity (U) is less than the average cross sectional velocity (U_{av}).

Turbulence can affect fish behaviour, and subsequently passage routes and attraction to fish passes (e.g. Silva *et al.*, 2011; Piper *et al.*, 2013). However, a number of flume based experiments have demonstrated that the behavioural response to turbulence is complex (e.g. Pavlov and Lupandin, 1994; Smith *et al*., 2005) and dependent on factors including species and their habitat preference, reproductive stage, hunger, and water velocity (reviewed in: Pavlov *et al.*, 2000). For example, juvenile rainbow trout preferentially selected a flume section with low turbulence and high velocity, until the mean velocity exceeded a threshold (0.24 and 0.40 m s^{-1} for small and large fish, respectively), at which point the high turbulence, low velocity channel was preferred (Smith *et al.*, 2005). Iberian barbel ascending experimental fish passes spent more time in areas of low velocity, low TKE and low horizontal shear stress (Silva *et al.*, 2011;

2012a). In contrast, European eel (A*nguilla anguilla*, L. 1758) approached experimental bar racks along the flume wall associated with the highest turbulence intensity (Russon *et al.*, 2010). In the field, elver passage at an intertidal eel ladder was more than twice as high when a plunging attraction flow was utilised compared to streaming flow, hypothesised to be at least partly due to attraction to turbulence (Piper *et al.*, 2012). Using behavioural response to turbulence to enhance fish pass efficiencies is likely to be highly complex, particularly for multiple species, and significantly more research is required to design favourable hydraulic conditions.

Velocity gradients are common at anthropogenic structures such as weirs, sluice gates and bypass entrances, where a constriction in the channel causes rapid flow acceleration, and at screens where deceleration occurs. A number of flume based studies have shown that some fish species respond to velocity gradients through a change in rheotaxis (e.g. Pacific salmon, Kemp *et al.*, 2005; 2006; brown trout, Russon and Kemp, 2011b) and/or upstream retreat (e.g. Haro *et al.*, 1998; Vowles *et al.*, 2014). This avoidance may be repeated several times before downstream passage occurs (Vowles *et al.,* 2014). Recent research suggests that salmonid response may be initiated at a threshold velocity gradient along the fish's body (Enders *et al.*, 2009; Russon and Kemp, 2011b; Vowles and Kemp, 2012; Vowles *et al*., 2014). For example, chinook salmon smolts responded to a decelerating velocity gradient at approximately 1 cm s^{-1} cm^{-1}, and to accelerating flow at a mean of 1.2 cm s^{-1} cm^{-1}, regardless of discharge (Enders *et al.*, 2012).

Little research into response to velocity gradients has been conducted for species other than salmon and trout. However, from the available data, the response of salmonid species to velocity gradients appears to be more pronounced than other fish. Although both American shad and Atlantic salmon swam against accelerating flow before passing experimental weirs, the latter had a higher passage rate at a modified weir (constant velocity acceleration over a long distance) than a sharp crested weir (rapid velocity acceleration), unlike American shad (Haro *et al.*, 1998). Research with European eel has shown mixed results. In a laboratory study, 95% of eels showed no response to a velocity gradient created by an orifice weir until physical contact with the structure, compared to 92.5% of trout reacting to the hydraulic conditions (Russon and Kemp, 2011b). However, 90% of migrating silver eels tracked at a hydropower intake channel, showed rejection (switch in rheotaxis and movement upstream > 2m) when the channel was constricted and velocity acceleration enhanced, compared to only 30% when the channel was open (Piper, 2013).

Historically, downstream migrating salmonid smolts were assumed to move passively with the flow (Cada, 2001). However, following the evaluation of unsuccessful bypasses and experiments into downstream moving fish response to hydraulic conditions (e.g. Haro *et al.,* 1998; Kemp *et al.*, 2005; 2006; 2008; Enders *et al.*, 2012) the principles of downstream bypass designs have changed, at least for salmonid species (Coutant and Whitney, 2000; Enders *et al.*, 2012; Williams *et al.*, 2012). Based on laboratory research into downstream moving salmonid behaviour, it is now commonly recommended that bypass entrances should accelerate smoothly to discourage retreat upstream (Larinier and Travade, 2002; Turnpenny and O'Keeffe, 2005).

Laboratory and field experiments on fish behavioural response to hydraulic cues have also led to recent advances in predictive modelling of fish swimming routes at anthropogenic barriers (Goodwin *et al.,* 2006). The Numerical Fish Surrogate model (Goodwin *et al.,* 2006) is an individual-based model that couples a Computational Fluid Dynamics (CFD) model of a dam forebay with simulated individual fish movements. Fish movements are based on the Strain-Velocity-Pressure hypothesis which combines response to total hydraulic strain (a measure of flow field distortion), velocity magnitude, and hydrostatic pressure to select a swimming path. Although behaviour may be influenced by other environmental and biological factors, including light, the presence of conspecifics or predators, and olfactory cues, in the complex hydraulic environment of dam forebays it is believed likely that hydrodynamic cues will dominate behavioural decisions (Goodwin *et al.*, 2006). This type of model could lead to improvements in determining suitable locations for bypass entrances, however, effectiveness ultimately depends on a good understanding of a range of species behaviour (Baigún *et al.*, 2007).

2.3. Quantitative review of the fish swimming performance literature

2.3.1. Methods

A quantitative review of the fish swimming performance literature was conducted using predefined search criteria to catalogue all relevant studies. Using a standardised method to search the literature minimises the subjectivity common in narrative ecological reviews (Arnqvist and Wooster, 1995; Roberts *et al.*, 2006). In addition, the unbiased database created can subsequently be used to ascertain trends and gaps in the literature (e.g. Haxton and Findlay, 2008; Roscoe and Hinch, 2010). Therefore, search phrases were created from combinations of the terms ‘fish’, ‘swimming’, ‘ability’, ‘performance’, ‘behaviour’, and ‘fish pass’. These were used to interrogate the internet search engines Web of Science, Scirus and Google Scholar, for English language peer reviewed journal articles. A full search was conducted in July 2010 and the database updated in September 2011. As a comprehensive examination of the grey literature (e.g. government reports, theses and conference proceedings) is limited by the availability of results to external organisations (Benzies *et al.*, 2006), this was not included. However, these studies were occasionally drawn upon in the discussion. All abstracts were examined and papers presenting original data on the swimming performance of species which inhabit freshwater lotic ecosystems for at least part of their life cycle were entered into the database. Any data on fish swimming performance can be applied to fish pass velocity criteria, regardless of the original motivation for collection (e.g. Leavy and Bonner, 2009). Therefore, it was not deemed necessary for the research to have been conducted with the intention to apply the results to fish pass design.

Studies entered into the database were categorised based on: the date of publication; location of research; motivation for research; the life stage, species and life cycle of fish studied; the methodology applied; and whether behaviour was evaluated (Table 2.1). By examining the study aims the motivation for research was split into whether or not the study was designed for application to fish pass, screen or culvert velocity criteria. Methodology was categorised dependent on whether field or laboratory based trials were conducted, the swimming mode (sprint, burst, prolonged or sustained) evaluated, apparatus used during laboratory studies (swim chamber, flume [including experimental fish pass] or other), and the performance protocol applied if a swim chamber was used

(U_{crit}, U_{max} or fixed velocity). Other apparatus was used infrequently and included fish wheels and still water test areas. If fish behaviour was also quantified then the factors evaluated were classified into:

- Swimming speed choice;
- Adaptations to reduce energy expenditure (i.e. time spent in different hydraulic patches, station holding, and swimming gait);
- Attraction (quantified through attempt rate, approach efficiency, channel choice tests, or passage delay).

An additional Chinese language search for fish pass motivated swimming performance studies was conducted by colleagues at the Institute of Hydroecology, Ministry of Water Resources, Wuhan, China. Following the finding that very few peer reviewed journal articles had been published on this topic, it was decided to also include any grey literature available to better determine gaps in the literature. The implications of including the grey literature are considered in the discussion.

Table 2.1. The categories recorded for each variable documented in a quantitative review of the fish swimming performance literature, using English language peer reviewed journal articles.

Variable	**Categories**
Date of publication	Year
Location of research	Continent
Fish life stage	Juvenile / adult
Fish species	Family
Fish’s life cycle	Anadromous / catadromous / potamodromous
Motivation for research	Fish pass design / other
Experimental method	Field / laboratory
Swimming speed category	Sprint / burst / prolonged / sustained
Laboratory apparatus	Swim chamber / flume / other
Swim chamber protocol	U_{crit} / U_{max} / fixed velocity
Swimming behaviour	Yes / No
Aspect of behaviour	Swimming speed choice / energy saving adaptations / attraction.

2.3.2. Results

A total of 225 papers quantifying fish swimming performance were identified between 1924 and 2011. The motivation for 48 (21%) of the articles was to inform fish pass design. There was a steady increase in the number of studies published annually after the 1980s and the majority were published after 2000 (Fig. 2.6). Of those motivated by fish pass design, 63% were published after 2000.

The majority of studies were conducted in North America (68%) or Europe (20%), while research from Australasia, Asia, South America and Africa accounted for 6, 5, 1, and 0% of the total, respectively. Publication occured after 2000 for 86% of the research conducted in Australasia, Asia and South America (Fig. 2.7). Of the 48 articles motivated by fish pass design, data collected in North America, Europe, Australasia and South America accounted for 69%, 15%, 10% and 6% of the articles respectively. The only three articles within the total database from South America were motivated by the design of fish pass facilities, yet none from Asia.

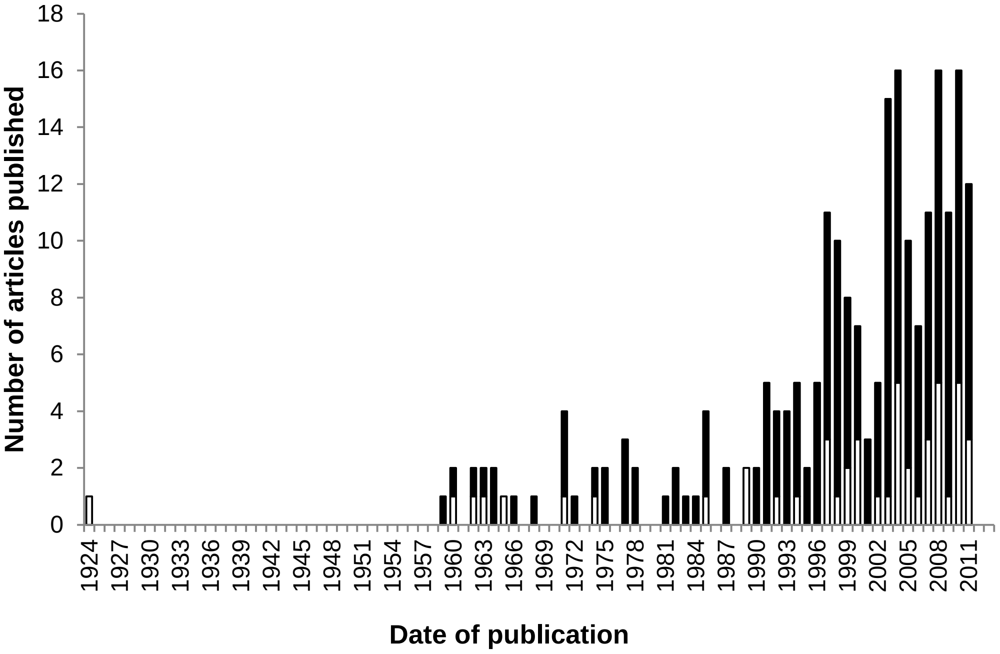


Figure 2.6. The number of English language journal articles quantifying fish swimming performance published annually, between the earliest identified (in 1924) and September 2011. The frequency is split into research that was (clear bars) and was not (black bars) motivated by application to fish pass design.

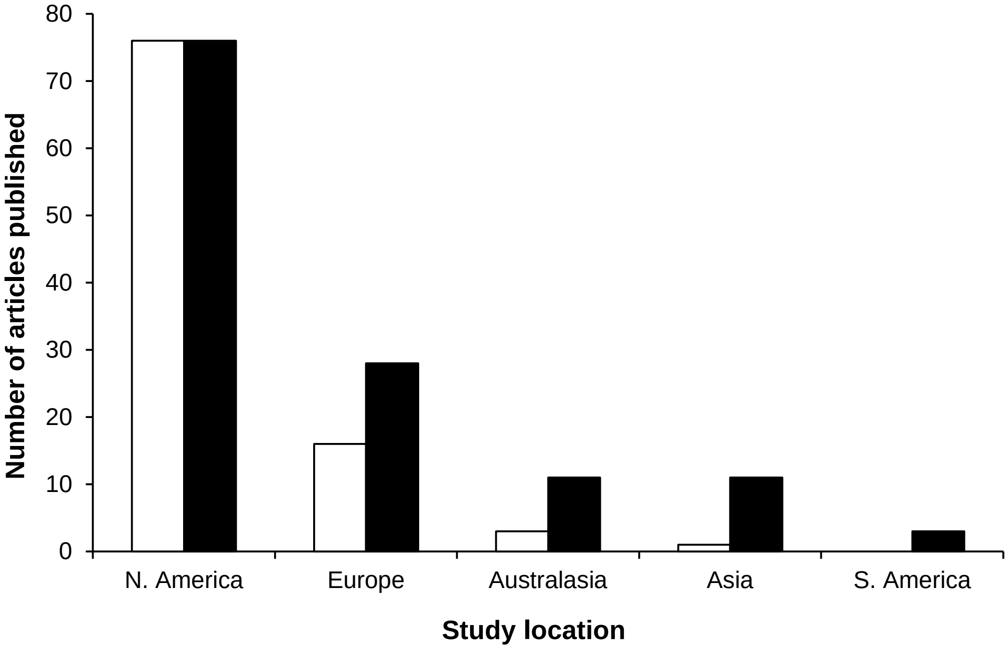


Figure 2.7. The frequency of English language journal articles quantifying fish swimming performance published per continent, prior to (clear bars) and after (solid bars) the year 2000 (last date of publication = September 2011). No studies were identified from Africa.

Juvenile fish were included in 57% of research and adults in 47%. Of those studies motivated by fish pass design, adults accounted for a greater proportion of the literature (77%, compared to 35% including juveniles). Members of the salmonidae family were included in 49% of all studies while cyprinidae, the next most studied family, were included in 16% (Fig. 2.8a). The anguillidae, centrarchidae, percidae, catostomidae and acipenseridae were the only other families included in more than 10 studies each. When the motivation for research was the design of fish pass facilities, the salmonidae family also dominated the data and were included in 25% of studies; however, the distribution between families was more even than across the whole database (Fig. 2.8b). The contribution of salmonidae to all studies decreased from 62 and 61% in the 1980s and 90s, respectively, to 42% in the 2000s, and 18% of the 28 articles published since 2010. For those studies focused on fish pass design the same trend occurred (Fig. 2.9).

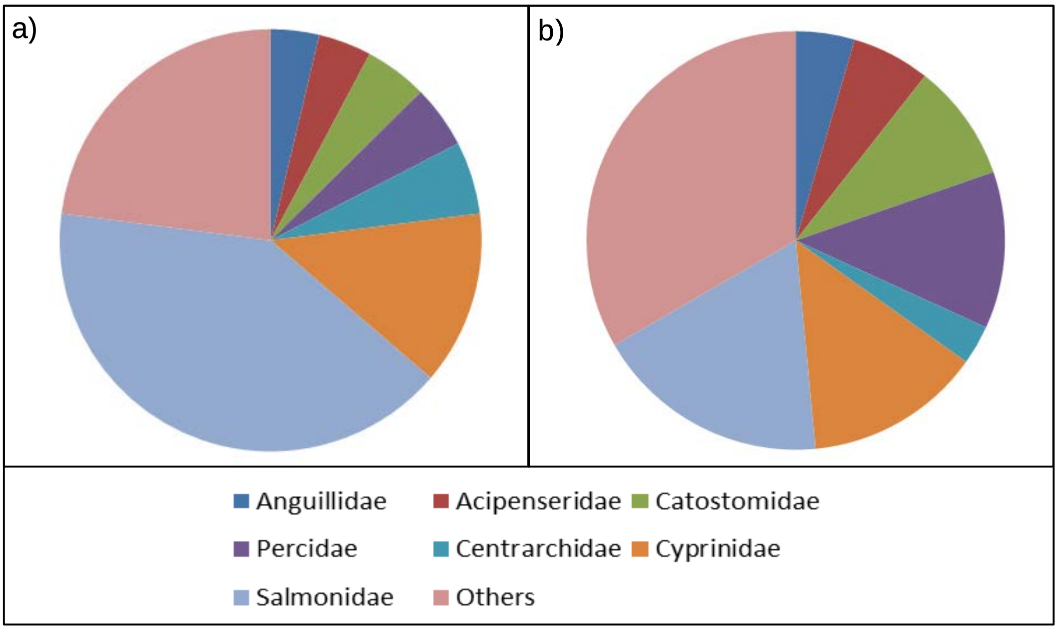


Figure 2.8. The proportion of English language journal articles published between 1924 and September 2011 quantifying fish swimming performance that included the most frequently studied families (included in at least 10 articles from the full database), from: a) the total database (n = 225); and b) those studies motivated by fish pass design (n = 48). All other families (included in < 10 published articles from full database) are included as 'others'.

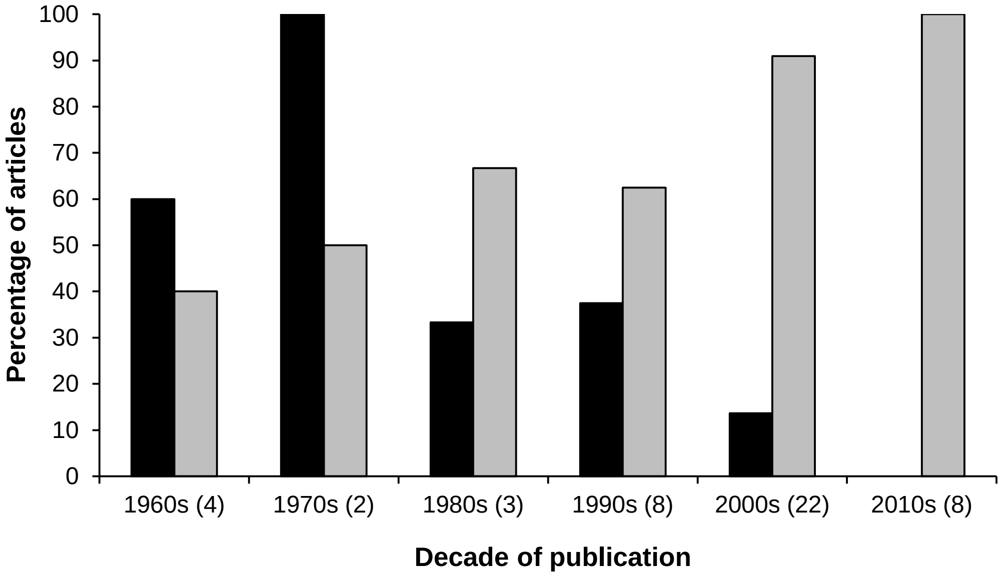


Figure 2.9. The percentage of English language publications quantifying fish swimming performance and motivated by fish pass design that included salmonid (black bars) and non-salmonid (grey bars) fish species, during each decade since the 1960s (up to September 2011). The number of publications is included in parenthesis.

Anadromous, catadromous and potamodromous species were included in 53, 7 and 47% of all studies, respectively (some studies included a mix of species). If research was motivated by fish pass design, catadromous species remained least studied (13%), and potamodromous and anadromous species were included in 56% and 50% of articles, respectively. Of the fish pass motivated research, there was a decrease in the inclusion of anadromous species since the 1970s, and potamodromous fish accounted for an equal or higher proportion than anadromous species since the 1980s (Fig. 2.10).

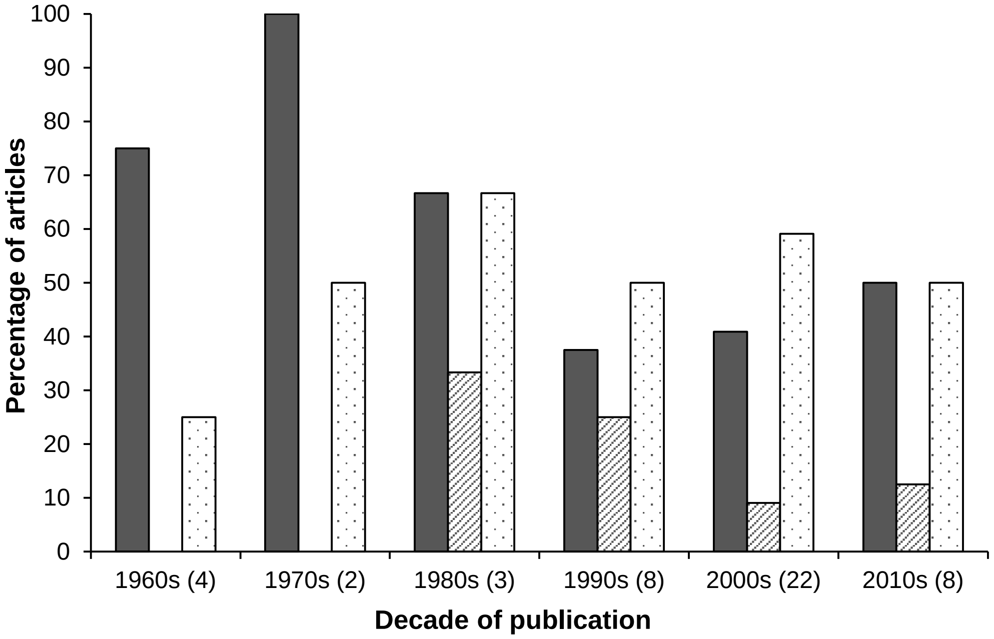


Figure 2.10. The percentage of English language publications quantifying fish swimming performance motivated by fish pass design, that included anadromous (grey bars), catadromous (striped bars) and potamodromous (dotted bars) species. Results are split into decade of publication from the 1960s (only 1 study identified prior to this in 1924) to September 2011. The number of publications identified per decade is included in parenthesis.

Five articles quantified fish swimming performance in the field, either by recording fish pass ascent (e.g. Bunt *et al.*, 1999; Macdonald and Davies, 2007) or using acoustic telemetry in still water (Arrhenius *et al.*, 2000; Hanson *et al.*, 2007). The remaining 220 studies were laboratory based. Swim chamber trials dominated the laboratory research and were included in 82% of these articles. The U_{crit} method was most common in swim chamber based research (83%), the fixed velocity test was used in 25% and the constant acceleration test in 4%, with several studies using a mix of two or more methods. Trials using open channel flumes and other equipment were included in 15% and 10% of publications, respectively. Flume based research was only conducted in North America (79%), Europe (12%) and Australasia (9%), and publication of this type of research increased after 2000 (Fig. 2.11a).

Of the 48 studies motivated by fish pass design, 94% were conducted in laboratory conditions. Swim chamber based evaluations of performance were included in 55% of these, of which 80% included the U_{crit}, 52% the fixed velocity, 12% the sprint test and none the constant acceleration method. Open channel flumes and other methods contributed to 51% and 9% of the laboratory studies motivated by fish pass design, respectively. The proportion of publications including flume based methods and motivated by fish pass design was generally higher in the last decade (Fig. 2.11b).

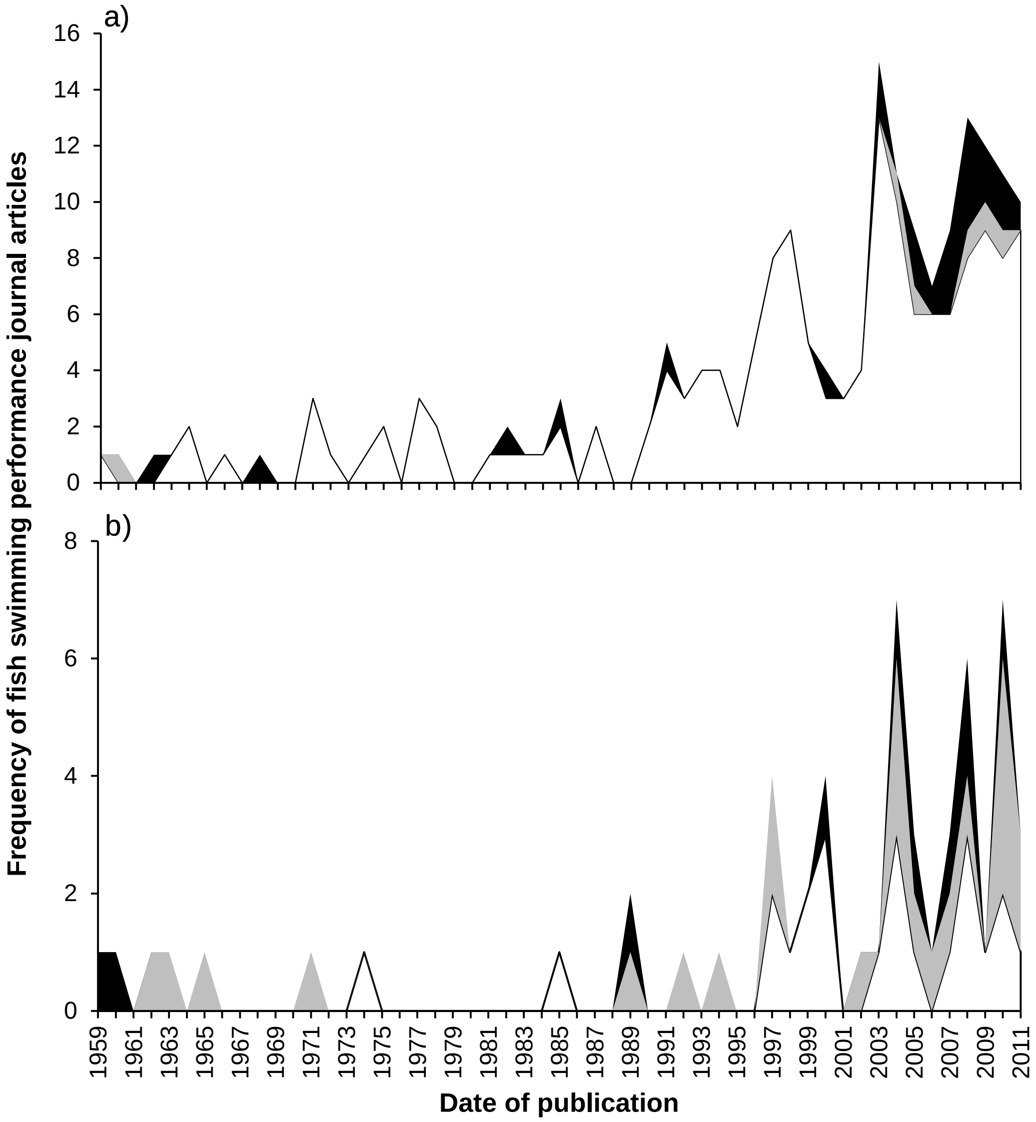


Figure 2.11. The number of English language journal articles published annually between 1959 and September 2011 that included swim chamber (clear), open channel flume (grey) and other (black) methods to quantify fish swimming performance. Articles are split into a) non fish pass related research (*n* = 176); and b) studies motivated by the design of fish pass facilities (*n* = 48). Other methods included field studies, fish wheels and still water raceways or tanks. Only one publication was identified prior to 1959 which was a field based study from 1924.

Due to the dominance of the U_{crit} test, prolonged swimming speeds were the most studied, and were included in 85% of all studies (Fig. 2.12). Burst and sustained swimming speeds were quantified in 27% and 12% of studies, respectively. For the latter, swim chamber tests dominated (86%), compared to a more even split for burst speeds (43, 41 and 16% using swim chamber, open channel flume and other equipment, respectively). Sprint speeds were always assessed in tanks and still water raceways.

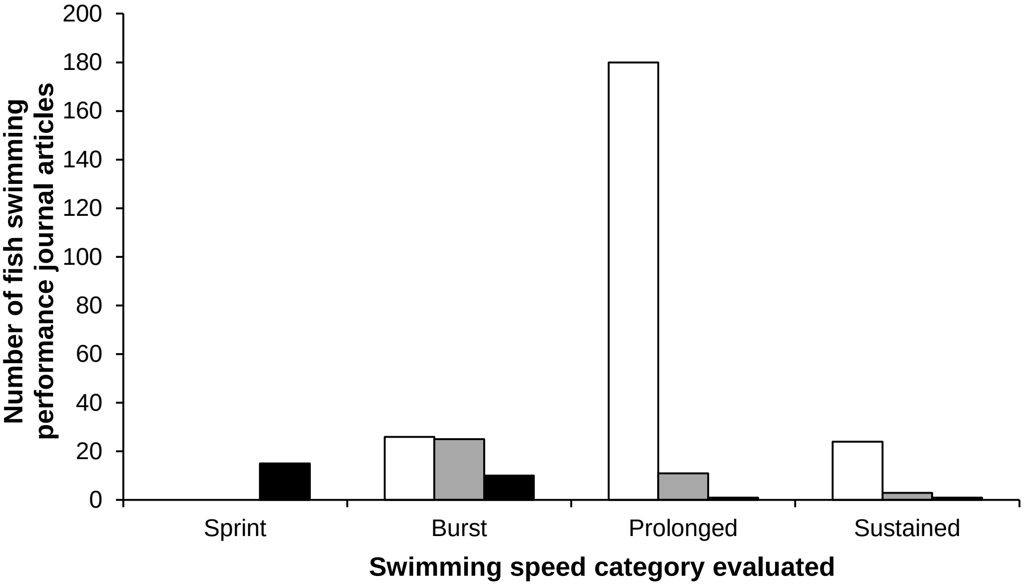


Figure 2.12. The number of English language journal articles found in a quantitative review of fish swimming performance that included a quantification of sprint, burst, prolonged and sustained swimming performance using swim chamber (clear), open channel flume (grey) and other (black) methodologies. Other methodologies included still water chambers and field studies. More than one method and swimming speed could be included per publication.

Fish swimming behaviour was quantified in 33 of the performance articles, equivalent to 15% of all studies, and 46% of those motivated by fish pass design. Two were *in situ* fish pass or culvert evaluations and the remainder were laboratory based. In eight of the latter, swim chambers were used for traditional swimming performance trials and the occupation of low velocity patches, swimming gait choice, or station holding behaviour quantified. However, the majority of studies (70%) including behavioural evaluation were completed in open channel flumes (Table 2.2). Furthermore, 70% were published after 2000 and all were completed in North America (76%), Europe (18%) or Australasia (6%). Members of the salmonidae and cyprinidae families were included in 24 and 21% of these studies, respectively, and acipenserids, catostomids and percids in 15% each (Fig. 2.13).

Table 2.2. The number of English language peer reviewed journal articles published between January 1924 and September 2011 that quantified fish swimming performance and also contained an evaluation of swimming behaviour. The behaviour studied was categorised into three groups and split into whether flume or swim chamber based methodologies were used (n = 33). Each paper may include one or more behavioural type.

Behavioural variables studied	Flume	Swim chamber	Field
Swimming speed choice	13	0	0
Energy saving behaviour	11	8	1
Attraction	7	0	1

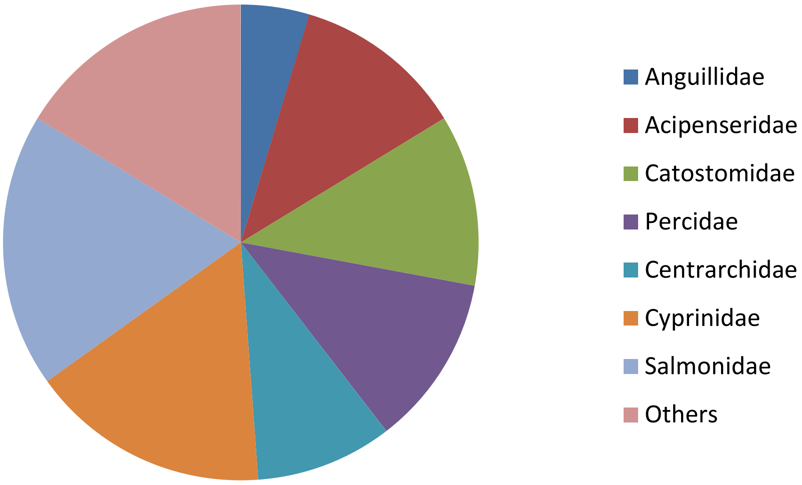


Figure 2.13. The percentage of English language articles that studied fish swimming performance and included an evaluation of behaviour (n = 33) which included the most commonly tested families of fish (included in > 10 swimming performance studies from the full quantitative review database of 225). Articles were published between January 1924 and September 2011. ‘Others’ includes all fish families evaluated in < 10 of the total 225 swimming performance publications.

Two studies completed in China were included in the English language quantitative review. These evaluated the swimming performance of the southern catfish (*Silurus meridionalis*, Chen 1977), grass carp (*Ctenopharyngodon idellus*, Valenciennes 1844), goldfish (*Carassius auratus*, L. 1758) and darkbarbel catfish (*Pelteobagrus vachelli*, Richardon 1846) using the U_{crit} test, but were not motivated by fish pass design (Fu *et al.*, 2009; Pang *et al.*, 2010). Two further journal articles and one book chapter in Chinese were found quantifying swimming performance to inform fish pass design. The book chapter presents research from the Nanjing Hydraulic Research Institute (NHRI, 1982) and includes the U_{crit} of eight species over a range of sizes (1-3 individuals per species). It also contains observations of five species (1 or 2 replicates each) ascending a model vertical slot fish pass, and the time taken to ascend a section of this (NHRI, 1982). Zhao and Han (1980) attempted to explore the relationships between body length, temperature and U_{crit} for seven species but used less than 5 individuals of each species and only one replicate per temperature treatment. This study also compared forced data to maximum velocities present during fish pass ascent (5 species, 1-3 individuals). In the other Chinese journal article data from fixed velocity tests were used to calculate the swimming ability index for seven species (Guan *et al.,* 1981) and to predict maximum distance of ascent at various water velocities. In total, the literature from China included data on the swimming performance of 15 species, from 5 families (summarised in Table 2.3). The critical velocity was assessed in two studies for the southern catfish, Wuchang bream (*Megalobrama amblycephala*, Yih 1955), common carp, silver carp (*Hypophthalmichthys molitrix*, Valenciennes 1844) and grass carp (Zhao and Han, 1980; NHRI, 1982; Fu *et al.*, 2009; Pang *et al.*, 2010), but only the English language studies included multiple replicates per treatment condition.

Table 2.3. Summary of the data presented in the English and Chinese language fish swimming performance studies conducted in China between 1924 and September 2011, detailing the species studied and the methods used to evaluate performance; this was either through a critical velocity test (U_{crit}), fixed velocity test (endurance), the maximum velocity found in fish passes during ascent (fish pass), or the time to ascend a section of model fish pass (model).

Species	Common name	Family	Life history	Methodology	Reference
Anguilla japonica	Japanese eel	Anguillidae	catadromous	fish pass	Zhao & Han, 1980
Carassius auratus	Crucian carp	Cyprinidae	potamodromous	U_{crit}, endurance, fish pass	Fu *et al*., 2009; NHRI, 1982; Zhao & Han, 1980; Guan *et al*., 1981
Coilia ectenes	Japanese grenadier anchovy	Engraulidae	anadromous	fish pass	Zhao & Han, 1980
Ctenopharyngodon idella	grass carp	Cyprinidae	potamodromous	U_{crit}, endurance, fish pass, model	Fu *et al*., 2009; NHRI, 1982; Zhao & Han, 1980; Guan *et al*., 1981
Culter erythropterus	predatory carp	Cyprinidae	potamodromous	U_{crit}, endurance, fish pass	NHRI, 1982; Zhao & Han, 1980
Cyprinus carpio	common carp	Cyprinidae	potamodromous	U_{crit}, endurance, fish pass	NHRI, 1982; Zhao & Han, 1980; Guan *et al*., 1981
Hypophthalmichthys molitrix	silver carp	Cyprinidae	potamodromous	U_{crit}, endurance, model	NHRI, 1982; Zhao & Han, 1980; Guan *et al*., 1981
Hypophthalmichthys nobilis	bighead carp	Cyprinidae	potamodromous	endurance, model	NHRI, 1982; Guan *et al*., 1981
Megalobrama amblycephala	Wuchang bream	Cyprinidae	potamodromous	model	NHRI, 1982; Zhao & Han, 1980
Mylopharyngodon piceus	black carp	Cyprinidae	potamodromous	endurance, model	NHRI, 1982; Zhao & Han, 1980; Guan *et al*., 1981
Ophicephalus argus	snakehead	Channidae	potamodromous	U_{crit}, endurance	NHRI, 1982; Zhao & Han, 1980
Parabramis pekinensis	white Amur bream	Cyprinidae	amphidromous	endurance	Guan *et al*., 1981
Siluris asotus	Amur catfish	Siluridae	potamodromous	U_{crit}, endurance	NHRI, 1982
Silurus meridionlis	southern catfish	Siluridae	potamodromous	U_{crit}, endurance	Fu *et al*., 2009; Pang *et al*., 2010
Trachidermus fasciatus	roughskin sculpin	Cottidae	catadromous	fish pass	Zhao & Han, 1980

2.3.3. Discussion

This quantitative review confirmed a historic bias in the fish swimming performance literature towards temperate species, especially salmonid species, and the use of swim chamber based methodologies. However, within the last two decades there has been an increase in journal publication of English language swimming performance research conducted outside of North America and Europe. In addition there has been an overall increase in the proportion of research using open channel flumes and including non-salmonid and potamodromous species. Although behavioural quantification was only included in a small proportion of the swimming ability research and was dominated by European and North American authors, publications including this have also increased since the beginning of the 21st century and were less biased towards salmonid species than the overall database.

Since the end of the twentieth century there has been an enhanced understanding of the migratory requirements of potamodromous fish (Lucas *et al.*, 1999; Lucas and Baras, 2001), the introduction of new legislation to protect non-salmonid temperate species (e.g. the EU Water Framework Directive; EC, 2000), and more research to improve fish pass designs in tropical countries (Thorncraft *et al.*, 2005; Mallen-Cooper, 2007). The same time period has seen an increase in fish pass effectiveness studies (Roscoe and Hinch, 2010). This study shows a concurrent increase in the publication of swimming performance articles, including those motivated by fish pass design (63% of the latter published between 2000 and 2011). Direct connections between publication date and drivers of research are not possible due to submission and publication delay between the collection of data and publication, which can reach two or more years (Kareiva *et al.*, 2002; O'Donnell *et al.*, 2010). Furthermore, the internet based search method could potentially create a bias towards more recent studies. However, the overall expansion in research this century (Fig. 2.6) has likely stemmed at least in part from a greater awareness of fish pass limitations and the need to improve designs for multiple species.

The findings of this quantitative review may be influenced by the exclusion of grey literature from the English language section (Conn *et al.*, 2003). Although many reviews and meta-analysis do not include grey literature, due to the large costs and time required to identify and retrieve these studies, its inclusion in medical meta-analysis can significantly change the results and conclusions (McAuley *et al*., 2000; Hopewell *et al*., 2007). However, the current systematic review was not designed to draw conclusions from the results, simply to evaluate trends in research areas and methods. As suggested by Roscoe and Hinch (2010), it is likely that the methods used in the grey literature will reflect trends in the more widely available published literature at the time. Therefore, the use of flume and swim chamber based methods to evaluate swimming performance is likely to be similar between sources. Furthermore, based on the requirement for novel research in peer reviewed journals, it is perhaps more likely that research into less studied fish species and including novel behavioural aspects of performance will be published here. It was therefore concluded that gaps highlighted in the review are likely to be true across the published and grey literature. However, before further research was conducted this was confirmed through a detailed review of the area of interest using all sources (see introduction of results chapters). The Chinese language grey literature studied very similar species and used similar methodologies as the published research. The inclusion of the grey literature book chapter alongside peer reviewed data did not alter the broad trends found, but ensured that a fuller assessment of the Chinese literature was conducted on which to base research aims.

Many fish passes installed for salmonid species have recently been evaluated for other fish, and efficiencies less than 50% are common (e.g. Bunt *et al.*, 1999; Moser *et al.*, 2002; Knaepkens *et al.*, 2006; Thiem *et al.*, 2011; 2013; Foulds and Lucas, 2013). A recent review found that, on average, the up and downstream efficiencies (attraction, entrance and passage combined) of all pass types was 62% (n = 31) for salmonids and 21% (n = 30) for non-salmonids (Noonan *et al.*, 2012). This discrepancy in efficiency is largely due to the historic bias towards salmonid swimming performance shown in this review (Fig, 2.8), and therefore the water velocities created in many traditional fish passes being unsuitable for weaker swimming species (e.g. Parsley *et al.*, 2007; Thiem *et al.*, 2011; Russon and Kemp, 2011a; Foulds and Lucas, 2013).

This study demonstrated an increase in non-salmonid swimming performance research over the last 20 years (Fig 2.9), to include fish species with a weaker swimming ability than salmonids, such as eel, sturgeon, lamprey and many cyprinids (e.g. Langdon and Collins, 2000; Dauble *et al*., 2006; Mateus *et al*., 2008; Hoover *et al*., 2011). For example, sturgeon swimming performance is limited by drag caused by their bony plates and poor thrust generation due to asymmetrical tail lobes (Webb, 1986; Peake *et al.*, 1997b; Peake, 2004b). Eel and lamprey species use an anguilliform mode of locomotion, characterised by large amplitude undulations along most of their body; this results in a weaker burst swimming performance than species employing a subcarangiform swimming mode using smaller and more posterior undulations with a more rigid body, such as salmon and trout (Breder, 1926; Gray, 1933; Lindsey, 1978; Sfakiotakis *et al.*, 1999).

Behavioural response of non-salmonids to hydraulic conditions has gained recent attention in both laboratory and field based research (e.g. sturgeon, Cheong *et al.*, 2006; lamprey, Keefer *et al.*, 2011; Kemp *et al.*, 2011; eel, Russon *et al.*, 2010; Russon and Kemp, 2011b; Piper *et al.*, 2012; 2013; Iberian barbel, Silva *et al.*, 2013). Many of these species have experienced recent population declines, and are protected by environmental legislation. For example, 17 of the world's 27 sturgeon species are critically endangered (IUCN, 2014) and there has been a dramatic decline in European, American (*A. rostrate*, Lesueur 1817) and Japanese eels (*A. japonica*, Temminck and Schlegel 1846) over the last three decades (Moriarty and Dekker, 1997; Haro *et al.*, 2000b; Tatsukawa, 2003).

In Europe, much of the more recently published non-salmonid swimming performance and behavioural research has been driven by EU legislation, including the Habitats Directive (Council Directive 92/43/EEC; EC, 1992), Water Framework Directive (Directive 2000/60/EC; EC, 2000), and the European Union council regulation number 1100/2007 for establishing recovery measures for the European eel (Eel Regulations; EC, 2007) (Lariner, 2008; Kemp and O'Hanley, 2010; Russon *et al.*, 2011; Piper *et al.*, 2012; Branco *et al.*, 2013). The Habitats Directive includes 65 fish species that must be kept at 'favourable conservation status' through protection of their habitats, including river and brook lamprey (*L. planeri*, Bloch 1748), Adriatic sturgeon (*Acipenser naccarii*, Bonaparte 1836), and bullhead (*Cottus gobio*, L. 1758) (EC, 2007). The Eel Regulations require member states to create eel management plans for achieving escapement to sea of 40% of silver eel biomass compared to that prior to anthropogenic impacts. The Water Framework Directive (WFD) expects 'good ecological status' to be met for all water bodies by 2015 (or good ecological potential if heavily modified). Physical modification, including barriers to fish migration, is a significant cause of current failure for many water bodies. Multi-species connectivity is therefore advocated to meet WFD targets as well as to protect species under the Habitats Directive and meet the Eel Regulations (P. Karageorgopoulos, pers. comm.).

Due to population declines since the 1980s, all but one study on eel swimming performance were published after this period. Yet only one used volitional open channel flume methods (Russon and Kemp, 2011a). This found that adult European eels could reach unexpectedly high burst swimming speeds to pass weirs. Volitional performance over a longer distance (> 1m) is yet to be evaluated. Despite the possibility that their elongated body will enhance susceptibility to destabilisation in turbulent flow (Liao, 2007) no research has explored its influence on swimming ability. Furthermore, an invasive parasite, *Anguillicoloides crassus* (Kuwahara, Niimi and Itagaki 1974), is believed to impact European eel migrations through a reduction in swimming performance (Sprengel and Luchtenberg, 1991), depleted swim bladder function (Barry *et al.*, 2014), and increased energy expenditure (Palstra *et al.*, 2007; reviewed in: Kirk, 2003). Although most research into this parasite has focused on the oceanic stage of migration, Sprengel and Luchtenberg (1991) hypothesised that a reduction in maximum swimming ability in infected fish could result in high entrainment at inlet screens. Thus, fish pass and screen velocity criteria based on mean swimming performance may not be suitable for parasitised individuals. Yet experimental studies exploring its effect on swimming performance have produced conflicting results (negative effect: Sprengel and Lüchtenberg, 1991; Palstra *et al.*, 2007; no impact: Nimeth *et al.*, 2000; Münderle *et al.*, 2004), and none considered potential behavioural impacts.

Temperate salmonid based fish pass designs were historically installed in many tropical countries, with little success for native fish species (e.g. Brazil: Oldani *et al.*, 1998; Mekong basin: Thorncraft *et al.*, 2005; Australia: Mallen-Cooper and Brand, 2007). The last 15 years have therefore seen an increase in native species research in many tropical countries (e.g. Russell, 1991; Mallen-Cooper, 1992; Mallen-Cooper and Brand, 2007; Dudgeon, 2005). The increased publication in Australasia and South America since 2000 (Fig. 2.9), reflects increased research into fish pass designs in these countries. In Australia such research has been successfully applied to adapting vertical slot and Denil fish passes by reducing slope and maximum water velocity (Stuart and Berghuis, 2002; Barrett and Mallen-Cooper, 2006; Mallen-Cooper and Stuart, 2007).

The same principle was applied at the Yangtang fish pass installed on the Mishui River, China, in 1980, which has low head drops (0.05 m) between pools, low velocity and minimal turbulence. Although the efficiency has not been quantified the pass is used by at least 45 fish species (Zhili *et al.*, 1990). However, many other fish passes installed between the 1960s and 80s were based on salmonid designs that failed to boost populations (Fu *et al.*, 2003; Dudgeon, 2005). New designs should therefore reflect the success of the Yangtang fish pass and utilise research on native species performance and behaviour. However, at present such data are seriously limited.

The number of Asian peer-reviewed ecological studies is limited compared to those conducted in western countries (Roscoe and Hinch, 2010; Martin *et al.*, 2012). Asian scientists only authored 1.6% of freshwater biology studies published in international English language journals between 1992 and 2001 (N = 4579), while less than 0.1% of the total addressed freshwater biodiversity conservation in Asia (Dudgeon, 2003). Replicating this trend, only 12 peer reviewed journal publications on fish swimming performance (5% of total) were identified from Asia in this English language quantitative review (Fig. 2.7). In addition, no English language swimming performance publications from Africa were identified and few from South America (Fig. 2.7).

The apparent lack of research from Asia, Africa and South America was certainly influenced by the exclusion of non-English language research (Moher *et al.*, 1996; Man *et al.*, 2004). Despite the rise of English language international journals globally, many scientists still publish in their native language in national publications (Meneghini and Packer, 2007). However, when Chinese language studies were included in this review, only three were discovered, making it possible to conclude that little swimming performance research has been conducted in China (Table 2.3). Similar conclusions are impossible for other countries without reviewing the native language literature. However, only14 publications (6% of total) were identified from English speaking Australia and New Zealand, the majority were conducted since 2000, and only 5 were motivated by fish pass design. Barriers are recognised as a significant contributor to fish population declines in these countries and fish pass installation is now common (e.g. Australia, Mallen-Cooper and Brand, 2007; New Zealand, McDowall, 2006). Therefore, it is somewhat surprising that there is limited swimming performance literature. This supportis the preliminary finding that swimming performance research is limited and recent outside of North America and Europe.

In China, past economic disparity has likely contributed to the deficiency in research, as willingness to act for conservation is generally higher during economic prosperity (Diekmann and Franzen, 1999; Stern, 2004). Environmental legislation also reflects this tendency, with the first in the UK established in the 1870s (Bell and McGillivray, 2005), compared to the 1970s in China (Ross, 1998). The limited legislation and complacency to act presents a constraint to the development of effective fish pass facilities in Asia (Dudgeon, 2005). However, some scientists across the country now recognise the constraints to developing new and effective fish passes in China due to the lack of ecological data to support designs (W. Xiang, pers. com.).

One paper from China used data from fixed velocity tests to calculate the swimming ability index (SAI). The SAI has been applied in Asia to compare swimming performance between fish species and body lengths assuming swimming ability is proportional to the area below the endurance curve (Tsukamoto *et al.*, 1975; Guan *et al.*, 1981). This metric accounts for combined sustained, burst and prolonged swimming, however, it has no direct application to fish pass design.

Cyprinidae account for 51.4% of China’s freshwater fish species (Kang *et al.*, 2014) and carp are the most commercially valuable species in China (Wu *et al.*, 1992). Their abundance and value are reflected by their dominance of the limited Chinese swimming ability literature (10 of the 15 species with identified data). In addition to the published literature, ongoing swimming performance research at the Institute of Hydroecology, Wuhan and the Three Gorges University, Yichang, aims to provide additional data for carp, and new data for species endemic to the Yangtze River basin, including the elongate loach (*Leptobotia elongate*, Bleker, 1870), Chinese sucker (*Myxocyprinus asiaticus*, Bleeker 1864) and largemouth bronze gudgeon (*Coreius guichenoti*, Sauvage and Dabry de Thiersant 1874). However, published and unpublished research to date has been limited by the body length and temperature ranges examined and the number of replicates. The Chinese language publications only studied one to three fish per species. As individual swimming performance can be highly variable (Kolok *et al.*, 1998; section 2.2), any conclusions drawn from this data are therefore subject to question due to the lack of replicates. Other swimming ability data were collected using poor methodologies. Volitional data were provided in oner study as time to pass an experimental fish pass, but only under one poorly quantified flow condition. In addition, swimming ability was estimated from maximum fish pass velocities, but it is unknown whether fish passed these high velocity areas. Some additional data, including high numbers of replicates, for bighead (*Hypophthalmichthys nobilis*, Richardon 1854) and silver carp also exist in the North American grey literature, where attempts are underway to control their spread as an invasive species (Layher and Ralston, 1997; Hoover *et al*., 2012).

There has been a recent criticism of applying swim chamber data to fish pass design, due to the conservative maximum swimming speeds reached and unrealistic flow conditions experienced (reviewed in: Plaut, 2001; Castro-Santos and Haro, 2006). This review shows that although the swimming performance literature is dominated by swim chamber based research (Fig. 2.11), these recent concerns are being accounted for. Chambers only accounted for half of the articles motivated by fish pass design and the overall proportion of publications including flume based research increased over the last two decades. Many of the later open channel flume studies also included non-salmonid and potamodromous species (e.g. Haro *et al.*, 2004; Peake, 2008; Russon and Kemp 2011a). In addition to facilitating performance enhancing behaviours, the greater area available in flumes compared to swim chambers enables the study of larger individuals and groups of fish. The proportion of flume based research may have contributed to the higher proportion of adult fish included in fish pass motivated studies than in the total dataset.

Despite the resurgence in open channel flume based swimming performance publications since the beginning of the 21st century, there were still only 33 articles identified using these methods. Large flumes are costly to construct and run compared to swim chambers, which may have contributed to their use being largely restricted to North America and Europe. Swim chamber studies, particularly the U_{crit} test, are quick and easy to conduct and remain popular even within fish pass motivated research. Swim chamber based research also continues to be valuable in understanding the effects of biotic and abiotic variables on swimming performance (e.g. parasite burdens and turbulent flow), and these findings should be considered during fish pass design. Furthermore, both this quantitative review and a recent collation of the swimming ability literature (Katopodis and Gervais, 2012) identified a bias towards the study of burst swimming speeds using flumes (Fig. 2.12). The only example of sustained swimming performance assessment within a flume was an ‘endless fishway’ experiment conducted in the 1960s (Collins *et al.*, 1962). Although burst speeds are crucial for passage of weirs, slots and orifices, complete ascent of a long fish pass could take several hours (Laine *et al.*, 1998), making prolonged and sustained swimming ability also of importance.

A mix of methodologies could be used to achieve a comprehensive understanding of unstudied species performance. An excellent example is provided by Bestgen *et al.* (2010) who evaluated the swimming performance of Rio Grande silvery minnow using U_{crit} and fixed velocity swim chamber trials, volitional passage success and D_{max} in an 18 m flume with various substrates, and ascent of experimental fish passes. Similar results between methods provided validation and confidence in the data not possible from one protocol alone; the mean U_{crit} was 0.52 m s^{-1}, endurance dropped suddenly between 0.50 and 0.60 m s^{-1}, less than 50% of fish successfully ascended the flume at 0.53 m s^{-1}, and successful fish had a mean swimming speed of 0.59 m s^{-1} (Bestgen *et al.*, 2010).

Although knowledge on the influence of turbulence on swimming ability, energetic costs and behaviour has increased since the 1990s (Lacey *et al.*, 2011), the range of species and turbulence characteristics for which data exist is still limited. The impact of turbulence on swimming performance has solely been researched in swim chambers. Therefore, open channel distance of ascent studies in turbulent flow could increase our understanding of fish performance under more natural conditions. The swimming ability studies in turbulent flow discovered in this review were conducted with non-salmonid species, as were a series of Russian studies on performance and behaviour (reviewed in: Pavlov *et al.*, 2000), however, research into energetics and habitat selection has focused on salmonids (e.g. Liao *et al.*, 2003a; Liao, 2004, Enders *et al.*, 2005a; b; Smith *et al.*, 2005; Cotel *et al.*, 2006). Many studies consist of a single eddy diameter shed regularly from cylinders (Webb, 1998; Liao, 2007), rather than the range of eddy sizes, orientation and vorticity found in rivers and fish passes. Furthermore, the intensity of turbulence created in laboratory tests is generally much lower than under natural conditions (Tritico and Hotchkiss, 2005; Lacey *et al.*, 2011).

The overall increase in publications containing flume based research and behavioural analysis since the turn of the century are inextricably linked and 70% of the studies including behavioural quantification were conducted in flumes (Table 2.2). Such research has increased our understanding of factors including: how behavioural adaptations assist in passing high velocity areas (Peake and Farrell, 2006; Kemp *et al*., 2009); the flow conditions that stimulate upstream movement (Castro-Santos, 2004; Cheong *et al.*, 2006); and how swimming speed selection influences passage success at velocity barriers (Castro-Santos, 2005). There appears to be a movement towards accounting for fish behaviour at passage facilities in the ecological literature (Nestler *et al.*, 2008; Rice *et al.*, 2010; Williams *et al.*, 2012), and 46% of the performance articles motivated by fish pass design included a behavioural aspect. Many gaps still remain however, and it is essential that collaboration occurs with engineers and government agencies to translate this research into improved designs.

2.4. Conclusions

Due to the limitations of assessing fish swimming performance in chamber conditions, further volitional research covering a range of species is required. However, a mix of chamber and open channel methods may be needed for a comprehensive understanding of the full range of swimming speeds. The narrative review demonstrated the importance of accounting for biotic and abiotic influences on performance. Both flume and chamber studies of performance are formed of micro-turbulent flow, yet mean water velocity is not the sole determinant of passage success (Larinier, 2002b). Fish may exploit low velocity boundary layers or recirculating flow to rest (Hoover *et al*., 2011; Kemp *et al.*, 2011), or conversely, destabilising eddies could increase the energy required for passage (Larinier, 2002b; Enders *et al*., 2005). Further research with a range of species should be conducted to understand fully the influence of turbulence on performance. It is also well known that intraspecific performance and behaviour can be highly variable, therefore factors other than temperature and body length may need to be accounted for during fish pass design.

The narrative review highlighted the importance of understanding both swimming ability and behavioural response to hydraulics for successful up and downstream fish passes. The consideration of behaviour during fish pass design is increasing, but data describing the response to common hydraulic conditions are unavailable for many species. Despite the increase in non-salmonid swimming ability research this century, parts of the behavioural literature are still dominated by salmon and trout. This bias is particularly true of research into response to velocity gradients, an important consideration in downstream bypass design. Only one peer reviewed experimental study with American Shad (Haro *et al.*, 1998) and one with European eels (Russon and Kemp, 2011b) have been conducted, and the effect of accelerating flow on eel behaviour remains unclear (Russon and Kemp, 2011b; Piper, 2013). A better understanding of multi-species behavioural response to turbulent flow, velocity gradients and low velocity patches is needed to increase attraction to fish pass entrances, reduce delay, and increase passage efficiency. Quantifying the behavioural response to well defined hydraulic conditions is easiest to achieve in controlled laboratory conditions, although field based validation is also necessary.

In Europe, the last two decades have seen an increased awareness of the passage needs of non-salmonid fish species. Yet data for many species remain less comprehensive than the historically well studied salmonids (Fig. 2.8). For example, despite a recent boom in eel swimming performance research, significant gaps remain, including the need for a better understanding of volitional swimming (see Russon and Kemp, 2011a for exception). Based on eel's ability to climb wet slopes with an irregular surface (Jellyman, 1977; Linton *et al.*, 2007), upstream passes using natural and synthetic climbing materials, including plastic bristles, netting and geotextile matting, have been in use across Europe since the 1980s (Knights and White, 1998; Thorncraft and Harris, 2000; Able, 2012). However, eel pass improvements have largely focused on upstream migration at dams and weirs, not culverts. Eels are also highly susceptible to mortality during turbine passage due to their elongated body morphology (Calles *et al.*, 2010). However, only recently have attempts been made to improve downstream bypass designs (Gosset *et al.*, 2005; Turnpenny and O'Keeffe, 2005; Larinier, 2008). In addition, there is little data available on the behavioural response of eels to the hydraulic stimuli created at barriers and fish passes (Fig. 2.13; for exceptions see, Russon *et al.*, 2010; Russon and Kemp, 2011b; Piper *et al.*, 2012; 2013).

Globally, there are still hundreds of fish species for which we have little or no knowledge. This lack of knowledge is particularly stark in tropical countries, including

China, where the species richness is high (962 freshwater fish species in China; Kang *et al.*, 2014). Dam construction is booming in China and it is essential that new fish passes are effective to prevent population collapse. Swimming performance research for Chinese fish species is limited and many species of economic and conservation importance lack reliable data (Table 2.3). None of the research to date (including unpublished studies; W. Xang, pers. comm.) has included quantification of behavioural response to hydraulic conditions such as turbulence and velocity gradients. As freshwater fish diversity is so high, it will be necessary to select target species with representative morphology, swimming ability, or behavioural position in the water column (Katopodis and Gervais, 2012) for research.

Chapter 3: Research aims and objectives

3.1. Aims and objectives

This thesis aims to advance the understanding of non-salmonid fish swimming performance and behavioural response to hydraulic conditions, to contribute towards improvements in multispecies fish pass designs. Objectives have been developed that contribute towards this broad aim whilst focusing on target species and areas of research identified in the literature review (Chapter 2). In this way the thesis will contribute directly to fish pass design criteria for species of conservation and economic concern, while also advancing existing knowledge of fish swimming performance and behaviour. Objectives are therefore to:

- Quantify the sustained, prolonged, and burst swimming performance of bighead carp (*Hypophthalmichthys nobilis*, Richardson 1854) using a range of laboratory based methodologies.

- Evaluate carp swimming behaviour in heterogeneous flow and its influence on performance.

- Determine the impact of wall corrugations on the swimming performance and behaviour of a juvenile cyprinid species.

- Evaluate the response of European eels (*Anguilla anguilla*, L. 1758) to an accelerating velocity gradient.

- Determine the relationship between the invasive parasites, *Anguillicoloides crassus* and *Pseudodactylogyrus* species, and the behavioural response of downstream moving silver eels to an accelerating velocity gradient.

- Assess the passage performance of upstream moving European eel in full-scale culvert models with different baffle designs.

3.2. Thesis overview

This section provides a brief overview of the remainder of this thesis and the rationale for the research questions addressed (summarised in Fig. 3.1). Research areas were based on the literature review results and supplemented by discoveries made throughout the experimental research.

Due to the historic bias towards salmonid based fish pass designs and research into their swimming ability and behaviour, this thesis focuses on non-salmonid fish species with different morphologies and life histories. The literature review demonstrated a lack of data on the swimming ability and behaviour of native Chinese fish species, which risks the current installation of fish passes being ineffective. Following discussion with colleagues in China the bighead carp was highlighted as a species of significant economic importance, for which fish pass design guidance is urgently needed. Juvenile bighead carp are widely impacted by anthropogenic barriers during migration from rivers to lakes. Yet, individuals used in the limited Chinese research were much larger (40 - 90 cm). Only one other study provided data for these small individuals, which was limited to 10 replicates with unclear methodology (Layher and Ralston, 1997). Therefore, Chapter 5 evaluates the swimming performance and behaviour of juvenile bighead carp between 5 and 20 cm long, using a range of methodologies.

Although research into the influence of turbulence on fish swimming ability and behaviour has increased in the last two decades, there are still considerable gaps in our knowledge (Chapter 2). Furthermore, despite the fact that weirs, baffles and corrugations all increase the intensities of turbulence, the design of fish pass facilities fails to adequately account for the impacts this can have on performance and behaviour. Attempts to account for flow heterogeneity and low velocity areas when setting velocity criteria in culverts are also based on limited behavioural data, with conflicting findings for different species and flow conditions. In Chapter 5 it was found that bighead carp only utilised low velocity areas at the flume edge during slow speed swimming, and it was suggested that turbulence may have influenced this behaviour. Therefore, fine scale analysis of the effect of corrugated walls and turbulence in the low velocity edge area on carp swimming performance and behaviour was conducted in Chapter 6.

The European eel was highlighted in the literature review as a species of significant conservation importance in the UK, with gaps remaining in research, particularly their response to hydraulic conditions associated with anthropogenic structures. Furthermore, although upstream bristle passes are well developed, downstream passage at dams and upstream movement through culverts are less researched and mitigation methods are poorly developed. Chapter 7 addresses the limited data on downstream moving eel behaviour. Using a fine scale laboratory method, response to accelerating flow was evaluated at velocities exceeding previous flume based studies. In addition, the influence of invasive parasites on their behaviour was evaluated, due to little current consideration of health on fish passage efficiencies.

The final results chapter (Chapter 8) utilises a more applied approach to evaluate European eel swimming performance and behaviour during a study to test the suitability of culvert baffles for improving upstream movement. Discussion with the Environment Agency highlighted the need for a baffle design that minimises debris accumulation, potentially using a sloping upstream face. A prototype baffle was therefore created and the hydraulic conditions induced and eel passage performance tested. As there is little evidence of eel passage through culverts or mitigation guidance on this topic, a common baffle design for salmonid species was also evaluated. Whilst this study had an applied aim to assess the effectiveness of baffle designs, it also allowed exploration of eel swimming ability and behaviour. Volitional swimming data over a longer distance (6 m) than already available (< 1 m) were collected and eel behaviour during culvert ascent observed. Although this research did not directly address the influence of turbulence on eel passage, turbulence intensities varied between baffle designs, with the potential to impact passage performance.

Chapter 9 draws together the results of this thesis to discuss advancements in our understanding of fish swimming ability and behaviour as well as recommendations for fish pass designs in China and the UK.

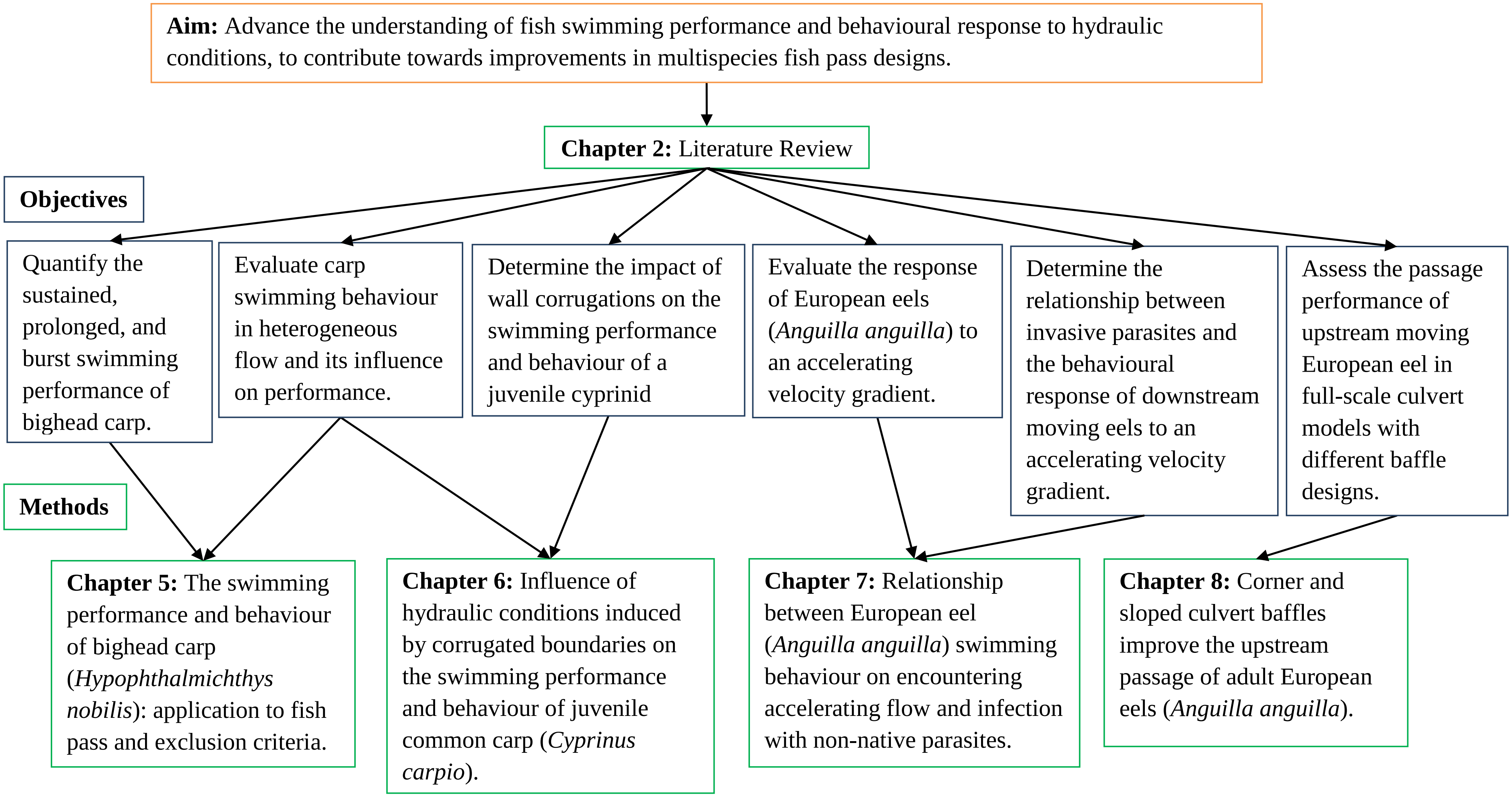


Figure 3.1. Schematic diagram of thesis aim and objectives, and the results chapters completed to meet these.

Chapter 4: Research Methodology

4.1. Introduction

This chapter provides an overview of the general methodologies employed to meet the thesis aims, and the rationale for their selection. This includes the species studied, equipment utilised, and the hydraulic and behavioural metrics quantified. In addition, practices to ensure good fish health and reliable data are outlined, and the technical specifications of laboratory equipment detailed. Full experimental methodologies are provided within each results chapter (Chapters 5-8).

4.2. Fish Species

4.2.1. European eel

The European eel (*Anguilla anguilla*, L. 1758) has a catadromous life cycle (Fig. 4.1). The larvae (leptocephali) drift from spawning grounds in the Sargasso Sea to the coast of Europe and North Africa. They arrive as transparent ‘glass eels’ (Schmidt, 1923; Tesch, 2003), transforming to ‘elvers’ following development of pigmentation. Most enter freshwater in the spring, and elvers then tend to migrate inland. Larger ‘yellow eels’ continue to disperse upstream, but in a more random process than elver colonisation (Ibbotson *et al.*, 2002; Feunteun *et al.*, 2003; Lasne and Laffaille, 2008). Yellow eels inhabit a range of aquatic habitats, including coasts, estuaries, rivers, lakes and wetlands (Tesch, 2003; Arai *et al.*, 2006), where they may remain for over 20 years before physiological and morphological transformation to the ‘silver eel’ stage. This metamorphosis includes a change in pigmentation to a more silvery underside and dark top side, an increase in pectoral fin and eye size, and development of the gonads (Lokmanl *et al.*, 2003; Durif *et al.*, 2005). Silver eels cease feeding to migrate downstream and swim the 5000 to 6500 km to spawning grounds in the Sargasso Sea within 6 months (van Ginneken *et al.*, 2005).

The European eel is of considerable social, economic and conservation importance (Tsukamoto and Kuroki, 2014; Kuroki *et al.*, 2014). Glass, yellow and silver eels are all commercially harvested for human consumption, and glass eels and elvers for aquaculture production (Nielsen and Prouzet, 2008). The annual EU eel catch was nearly 20,000 tonnes in the 1950s (ICES, 2012), but had declined to approximately 5,000 tonnes at the beginning of the 21st century, and 3,201 tonnes in 2011 (ICES, 2012). Despite this reduction, the export value of eels in England and Wales alone was still £3.5 million per annum at the end of the 20th century (Peirson *et al.*, 2001).

There has been a dramatic decline in the abundance of European eels over the last three decades, and recruitment of glass eels is now at 1 to 10% of pre-1980 levels (ICES, 2013). The International Council for the Exploration of the Sea (ICES) determined that the stock was 'outside safe biological limits' at the end of the 1990s and that European eel fisheries were unsustainable (ICES, 1999). In 2007 the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) listed the species in Appendix II (not threatened with extinction but may become so if trade is not controlled) and in 2008 their status was updated to critically endangered on the International Union for Conservation of Nature (IUCN) red list of threatened species (Freyhof and Kottelat, 2010). A range of factors have been implicated in contributing to this decline, during both the marine and freshwater life stages (Moriarty and Dekker, 1997; Feunteun, 2002). One potential cause of the decline is anthropogenic structures, which can block access to upstream habitat (White and Knights, 1997), cause mortality during turbine passage (Calles *et al.*, 2010) and delay downstream migration (Piper *et al.*, 2013). In response to the decline, the EU introduced Council Regulation No 1100/2007 for the recovery of European eel in 2007 (EC, 2007). This regulation required all member states to produce Eel Management Plans for each river basin containing natural eel habitat. The primary aim of these is to permit the escapement to sea of at least 40% of the silver eel biomass relative to that prior to anthropogenic influences. Plans include artificial stocking, fishing restrictions and measures to improve habitat access and quality. The Eel (England and Wales) Regulations 2009 implement the EU council regulation and provided the Environment Agency with the powers to enforce the construction of an eel pass at obstructions likely to impede passage and to ensure any facility abstracting more than 20 m^3 of river water a day (and likely to pose a risk to eels) is screened appropriately by January 2015.

To improve the data available on European eel swimming ability and behaviour experimental trials were conducted. Hatchery reared fish can be morphologically different to wild individuals (Swain *et al.*, 1991; Hawkins and Quinn, 1996) and tend to be adapted to slow flow and low turbulence conditions, which can result in a weaker swimming performance (McDonald *et al*., 1998; Handelsman *et al.*, 2010). Therefore, wild fish should be utilised during experimental trials where possible. European eels for this research were caught at an eel rack by a commercial silver eel fisherman (Chapter 7) and during Environment Agency electrofishing surveys (Chapter 8).

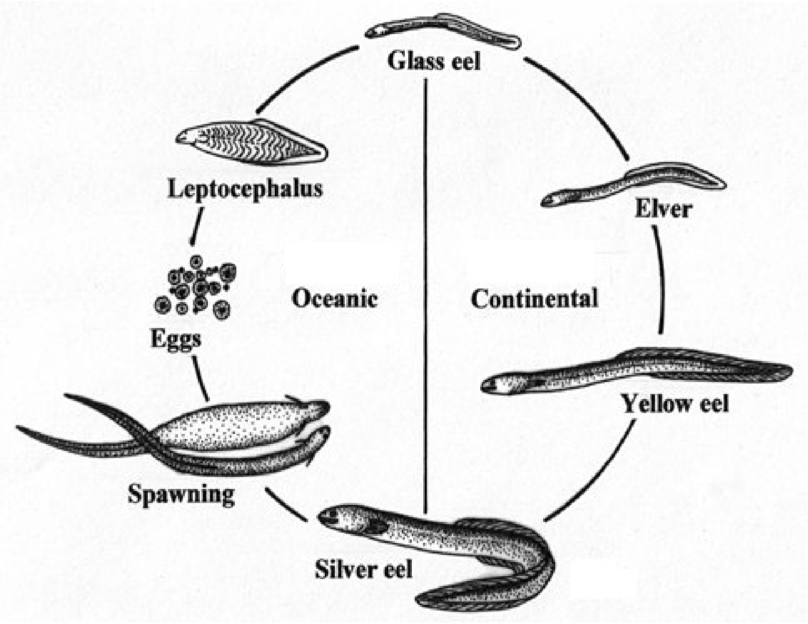


Figure 4.1. European eel (*Anguilla anguilla*) life cycle (Moriarty and Dekker, 1997).

4.2.2. Bighead carp

The bighead carp (*Hypophthalmichthys nobilis*, Richardson 1854) (Plate 4.1) is a potamodromous species native to China but introduced to many countries globally. In its native range, spawning occurs in the middle and upper reaches of rivers and is triggered by a peak in discharge and an increase in water temperature between May and July (Duan *et al.*, 2009). The semi-buoyant eggs and larvae then drift downstream, before larvae and juveniles move to lakes and other off channel habitats for rearing (Jennings, 1988). Bighead carp are one of the four most commercially valuable freshwater fish species in China, alongside silver carp (*H. molitrix*, Valenciennes 1844), grass carp (*Ctenopharyngodon idella*, Valenciennes 1844*)*, and black carp (*Mylopharyngodon piceus*, Richardon 1846). They also contribute to the country’s booming aquaculture industry, which in 2002 produced 1.7 million tonnes of bighead carp. This accounted for 98.7% of the global total, valued at US $1.48 billion (Weimin, 2014).

The abundance of bighead carp has declined substantially in their native range over recent years due to pollution (Dudgeon, 2002), overfishing (Zhong and Power, 2007), land reclamation (Fang *et al.*, 2006), capture for aquaculture (Chen *et al.*, 2004), and anthropogenic barriers. Large dams have flooded their historic spawning grounds (Duan *et al.*, 2009), changed river flood hydrographs (Yi *et al*., 2010), altered temperature and nutrient availability (Zhang *et al*., 2012), and blocked migration routes. In addition to impeding upstream migration, anthropogenic barriers have disconnected rivers from lakes, and caused injury and mortality to downstream moving fry (Zhong and Power, 1996; Ru and Liu, 2013). Similar pressures have affected the other economically valuable carp species and in the middle reaches of the Yangtze River the contribution of bighead, silver, grass and black carp to the total catch decreased from 80 to 90% in the 1960s to less than 5% at the end of the twentieth century (Chen *et al.*, 2004). In a similar trend, the contribution of these four carp species to the Dongting Lake fishing yield steadily declined from 21% in 1963 to 9.3% in 1999, during which time the yield of non-migratory species increased (Liao *et al.*, 2002; Fang *et al.*, 2006). In 2003 a three month fishing ban (April – June) was introduced to a 600 mile stretch of the middle and lower reaches of the Yangtze River to try and restore the stocks of many species, including bighead carp. In addition, hatchery reared bighead carp fry are released in lakes to replenish natural populations (Kangmin, 1999), and they are included as a target species for fish passes at many new dams (D. Han, pers. comm.).

In many areas of Europe, Asia, and North America, Bighead carp have been introduced as a food fish or for zooplankton and phytoplankton biocontrol in aquaculture ponds and wastewater treatment lagoons. Accidental and deliberate release to the wild has resulted in their establishment in over 20 countries, and an increased range within China (Kolar *et al.*, 2005). Their tolerance for a wide range of environmental conditions, particularly temperature (active between 10 and 30°C, spawn between 18 and 30°C) and turbidity, combined with a high fecundity and growth rate (Kolar *et al*., 2005), has aided their rapid spread across many countries. Bighead carp are a particular problem in the U.S. where they were introduced in the early 1970s and have been reproducing in the wild since the 1980s. They have now been reported in 23 states, are self-sustaining in the

Mississippi, Missouri, Ohio, and Tennessee River basins, and are within 50 miles of the ecologically sensitive Great Lakes system (Kolar *et al*., 2005). They have been shown to alter native food web interactions and have the potential to outcompete native planktivorous species, including the gizzard shad (*Dorosoma cepedianum*, Lesueur 1818), bigmouth buffalo (*Ictiobus cyprinellus*, Valenciennes 1844), and American paddlefish (*Polyodon spathula*, Walbaum 1792) (Schrank *et al*., 2003; Irons *et al*., 2007; Sampson *et al*., 2009). As a result, since the bighead carp catch has increased there has been a concurrent decline in the commercial buffalo catch (Conover *et al*., 2007).

The bighead carp was selected as a representative Asian carp species for research in this thesis. The dual problems of population decline due to barriers in China and the spread of invasive populations elsewhere, mean that swimming ability and behavioural data are required for successful fish pass and exclusion barrier design. The seasonal fishing ban on bighead carp was in force in China during the experimental period. Therefore, hatchery reared fish were used for trials (Chapter 5). It is recognised that velocity criteria based on the swimming performance of these individuals may be conservative and should be validated with wild individuals.

Plate 4.1. Juvenile bighead carp (*Hypophthalmichthys nobilis*) swimming in an open channel flume at the Institute of Hydroecology, Wuhan, China.

4.2.3. Common carp

Common carp (*Cyprinus carpio*, L. 1758) are a potamodromous species, native to areas of Europe and Asia but introduced throughout the world. They predominantly live in deep, slow flowing rivers or lakes and spawn in backwaters and floodplains (Flajšhans and Hulata, 2006). Common carp have a long history of domestication (Balon, 2004) and are still of considerable economic value in China, both within capture fisheries (Zhong and Power, 1997) and aquaculture (over 2.89 million tonnes produced in 2012 valued at $3.3 billion; FAO, FishstatJ database). They are often less impacted by hydropower developments than many carp species due to their preference for slower flowing habitats (Chen *et al.*, 2009). However, they are categorised as vulnerable on the IUCN Red List due to an estimated decline of over 30% in their native range, partly due to river regulation preventing long distance spawning migrations (Freyhof and Kottelat, 2008).

Common carp were selected for behavioural research in this thesis due their morphological similarity and comparable swimming ability to other Asian carp (Rome *et al.*, 1990; Boeck *et al.*, 2006; Tudorache *et al.*, 2007). A strain, known as mirror carp, were sourced from a local hatchery due to logistical constraints on obtaining large numbers of wild carp of a similar size. Although their swimming ability may have differed from wild individuals, the experiment was designed for relative comparisons between treatments rather than the direct use of capability data. Behavioural trends are likely to be comparable between wild and hatchery reared individuals, although the hydrodynamic thresholds at which a behavioural response is induced may differ. For example, both hatchery reared brown trout and wild salmonids exhibit an avoidance response to accelerating velocity gradients, but the threshold at which a reaction occurs is lower for hatchery reared trout, potentially due to a weaker swimming ability (wild, Kemp *et al*., 2005; Enders *et al*., 2009; hatchery, Russon and Kemp, 2011; Vowles and Kemp, 2012).

4.3 Fish handling

Fish were transported to research facilities in aerated holding tanks or oxygenated plastic bags within three hours of collection. On arrival they were gradually acclimatised to tank temperatures before transfer, which was thereby automatically recorded every hour. Fish were held at a stocking density of 1.2 to 26.5 kg m^{-3} in aerated and filtered tanks, filled with de-chlorinated municipal tap water. Water quality was monitored at least every two days and weekly water changes (approximately 10-20%) were conducted to help maintain low nitrate and nitrite concentrations and prevent ammonia accumulation. Cyprinid species were fed daily, but silver eels cease feeding following the onset of migration (Tesch, 2003), therefore no food was offered. Yellow eels would not accept food in captivity but appeared to be in good condition throughout the experimental period and were returned to their source river with zero mortality within 26 days. During analysis of eel behaviour and performance, the time spent in holding facilities was included in initial statistical tests, due to the potential for confinement to alter their health and migratory desire.

All individuals were allowed at least three days after transportation before trials began and were tested within five weeks of collection. Fish transfer between holding tanks and experimental equipment was fast and air exposure minimised. Prior to the beginning of trials an acclimation period was allowed to minimise the influence of stress on fish behaviour and experimental results (Portz *et al.*, 2006; Wilson, 2014). Mean tank and flume temperatures were within 2°C of each other throughout the study periods. Indoor flumes were screened with black material and observers remained at least 1 m away from other equipment to minimise disturbance. The University of Southampton ethics committee approved all experimental work and, where necessary, Home Office regulations and procedures were followed.

4.4. Experimental principles

Swimming ability can be evaluated in the field by measuring the water velocity during ascent of fish passes or other velocity barriers (e.g. Stringham, 1924; Belford and Gould, 1989; Bunt *et al.*, 1999). However, the exact position of fish and the hydraulic conditions experienced are not easy to determine, which can ultimately reduce the accuracy of results. Furthermore, when swimming ability is inferred from passage of a velocity barrier, differentiation of passage failure due to velocity exceeding swimming capability or an alternative factor, such as a behavioural avoidance of turbulence or water depth, is challenging. Therefore, laboratory analysis forms the vast majority of swimming performance research (Chapter 2) and is utilised in this thesis.

In terms of behavioural analysis, although methods to track fish in the field are improving, the most accurate 3D acoustic telemetry still has a resolution of up to 1 m (Brown *et al.*, 2009), compared to the ability to track fish on a sub cm scale using video recordings of laboratory trials (Enders *et al.*, 2009). Fine scale tracking and hydraulic evaluation can improve confidence in conclusions drawn from behavioural observations. For example, coarse scale telemetry data are unable to determine whether the avoidance response of eels at debris screens is due to hydrodynamic gradients or physical contact (Jansen *et al*., 2007). In addition, laboratory methods provide greater control over confounding variables and the ability to manipulate those of interest. This control over test conditions is essential to developing a transferable ecological rule base for fish pass design, rather than applying a site specific trial and error approach in the field (Rice *et al*., 2010). Although flume studies are criticised for the simplified channel and hydraulic conditions created, when applied to the development of artificial concreted fish passes this constraint is of less concern than for research into natural habitat use (Rice *et al.*, 2010). Both performance and behavioural data from laboratory studies should however be validated *in situ*. This thesis compares laboratory results with the field based literature, or recommends further study where this is unavailable.

Due to the benefits reviewed in Chapter 2 several experiments in this thesis focus on volitional swimming in open channel flumes (Table 4.1). However, to complement the flume based data and to compare volitional and forced swimming performance and behaviour, both a swim chamber and open channel flumes were used to evaluate bighead carp performance (Chapter 5). To improve our understanding of fish swimming performance and behaviour in non-uniform flow, hydraulic conditions associated with fish passes and anthropogenic barriers to migration (e.g. accelerating velocity gradients and turbulence) were created in other volitional studies (Chapters 6-8).

Temperature control was possible in the small flume and swim chamber used during much of the analysis with bighead carp (Chapter 5), therefore, it was maintained close to that experienced by juvenile bighead carp migrating from the Yangtze River to Poyang Lake (H. Maolin, pers. comm.). However, controlling temperature in a large flume is difficult and costly due to the volume of water and heat produced from the operation of hydraulic pumps (Kemp *et al*., 2011). During long experimental periods natural changes in the weather conditions also influenced temperature (e.g. 5 °C change in water temperature, Chapter 9). As temperature is well known to affect fish swimming ability (Wardle, 1980; Rome *et al.*, 1990) it was included as a covariate in all initial statistical models.

Although the behaviour of some species may be influenced by schooling (Haro *et al.*, 1998), and energetic advantages can be gained from swimming in schools (Ross *et al.*, 1992; Svendsen *et al*., 2003; Burgerhout *et al.*, 2013), individual fish were used in all trials. When analysing passage of a group it is often impossible to identify individuals, leading to complications in identifying successful fish if passage is followed by fall back downstream (e.g. Bestgen *et al.*, 2010). By tagging fish ascending a flume it is possible to analyse individual performance and behaviour within schools, however, the results are limited to passage success, distance of ascent and average swimming speeds, and it is not possible to identify specific areas and hydraulic conditions utilised without video analysis. In addition, testing individuals separately removed the influence of competition on swimming location, ensuring that behavioural observations were unrelated to conspecifics.

During open channel flume trials, swimming performance and behaviour were volitional and areas of low water velocity were present for refuge. Therefore, the time limit placed on trials could affect results by denying future attempts (Castro-Santos, 2004). However, a compromise had to be made between ensuring trials were long enough to observe realistic behaviour and performance, and having high numbers of replicates to account for intraspecific variation whilst minimising the time spent in captivity. Pilot trials of one hour were conducted to provisionally evaluate fish activity. If passage attempts were made quickly and success occurred within 30 min for 90% of the fish then trial length was reduced to 45 or 30 min.

Table 4.1. Summary of the experimental equipment and methods used during this thesis to assess the swimming performance and behaviour of European eel and carp species.

Fish species	**Equipment**	**Method**	**Swim speed category**	**Behaviour**	**Chapter**
Bighead carp	Swim chamber	Fixed velocity test	Sustained, prolonged, burst	NA	5
Bighead carp	Flume (1 m section)	Fixed velocity test	Sustained, prolonged, burst	Use of low velocity areas	5
Bighead carp	Swim chamber	Constant acceleration test	Prolonged	NA	5
Bighead carp	Flume	Volitional upstream passage	Burst	Approaches, ground speed	5
Mirror carp	Flume (1.3 m section)	Fixed velocity test	Prolonged	Use of low velocity areas	6
European eel	Flume	Volitional downstream passage	NA	Response to velocity acceleration	7
European eel	Experimental culvert	Volitional upstream passage	Burst	Number of entrances, delay	8

4.5. Laboratory apparatus

The 93 L swim chamber used for studying bighead carp swimming performance (Chapter 5) at the Three Gorges University, Yichang, had two working sections, allowing the simultaneous testing of two fish on opposite sides of the chamber (Plate 4.2). Each working section was 0.85 m long, 0.15 m wide and 0.15 m deep and had a removable wire mesh at the downstream end and a honeycomb screen at the upstream end. Flow was driven by a three phase electric motor to achieve a water velocity up to 0.82 m s^{-1}. A cross vane flow straightener and honeycomb cross sections downstream of the motor were used to create homogeneous flow conditions. The chamber was placed inside a buffer tank from which aerated water was exchanged. Water was changed weekly, using the municipal tap supply, to maintain good quality and clarity, and was aerated for at least 24 hours to remove chlorine prior to trials. Temperature was controlled in the buffer tank using water heaters and cold water exchange.

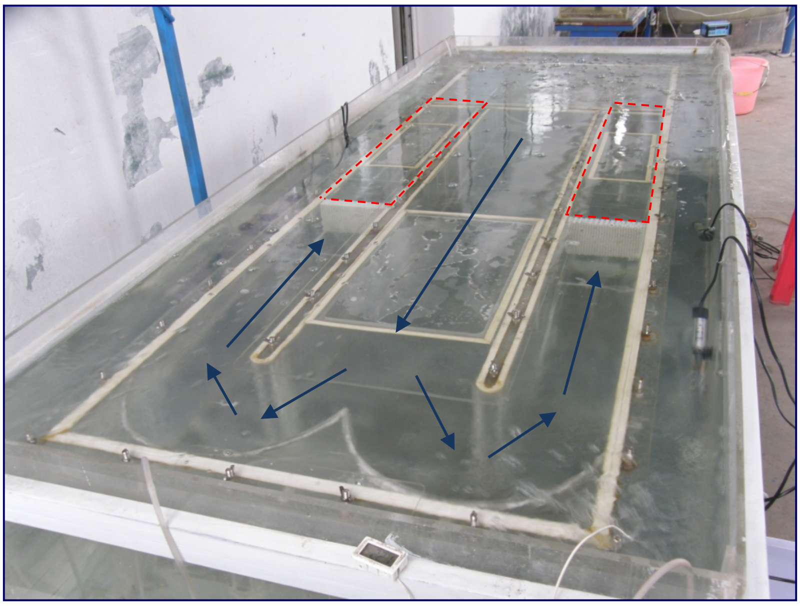


Plate 4.2. Swim chamber used for the evaluation of juvenile bighead carp swimming performance at the Three Gorges University, Yichang, China, using forced swimming methods. The two test sections are highlighted with red dashed lines and flow direction is shown by arrows.

Experiments on the swimming endurance of bighead carp in an open channel were conducted at the Institute for Hydroecology, Ministry of Water Resources, Wuhan, China. The large glass sided recirculating flume was 13.0 m long, 0.6 m wide and 0.8 m deep (Plate 4.3a). Water was circulated from a holding pond through the flume facility by up to three centrifugal pumps (5.5, 7.5 and 18.5 KW each). Velocity was controlled by the number of pumps in use and the height of an adjustable downstream weir. Volitional experiments with bighead carp at the Three Gorges University, Yichang, China, were conducted in a glass sided re-circulating oval raceway 6.5 m long, 0.4 m wide and 0.7 m deep (Plate 4.3b). The flume floor was covered in white plastic to improve the clarity of behavioural observations. The activation of four electric pumps controlled the water velocity passing through three flume constrictions (Plate. 4.3c). Water temperature was manipulated using water heaters, cold water exchange and air temperature regulation.

A large glass walled recirculating flume (21.4 m long, 1.4 m wide and 0.6 m deep) at the International Centre for Ecohydraulics Research (ICER) experimental facilities, University of Southampton, UK, was used for trials with mirror carp (Chapter 6) and evaluating European eel response to a velocity gradient (Chapter 7) (Plate 4.4a). The three centrifugal pumps (individual capacities = 0.09, 0.15 and 0.23 $m^3 s^{-1}$) had a maximum flow capacity of 0.47 $m^3 s^{-1}$. Velocity was controlled by adjusting the height of the downstream weir and manipulating the flow volume through activating different pumps. Passage performance and behaviour of European eel during ascent of an experimental culvert (Chapter 8) were studied in a concrete outdoor recirculating flume (trapezoidal channel: 50.0 m long, 2.1 m wide, 0.5 m deep) at the ICER experimental facilities (Plate 4.4b). The maximum flow rate was 0.80 $m^3 s^{-1}$ and velocity was manipulated by altering the height of a downstream weir and the activation of three centrifugal pumps with adjustable valves.

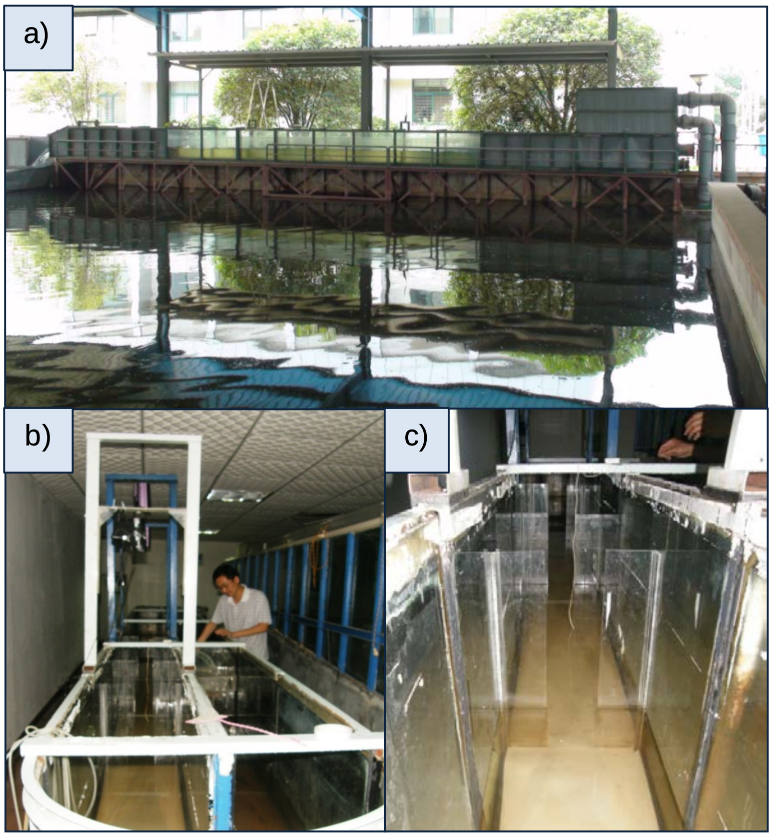


Plate 4.3. Open channel flumes used to study juvenile bighead carp swimming performance and behaviour in: a) a section of outdoor open channel flume at the Institute of Hydroecology, Wuhan and b) a recirculating oval raceway at the Three Gorges University, Yichang, using the channel constrictions illustrated in c.

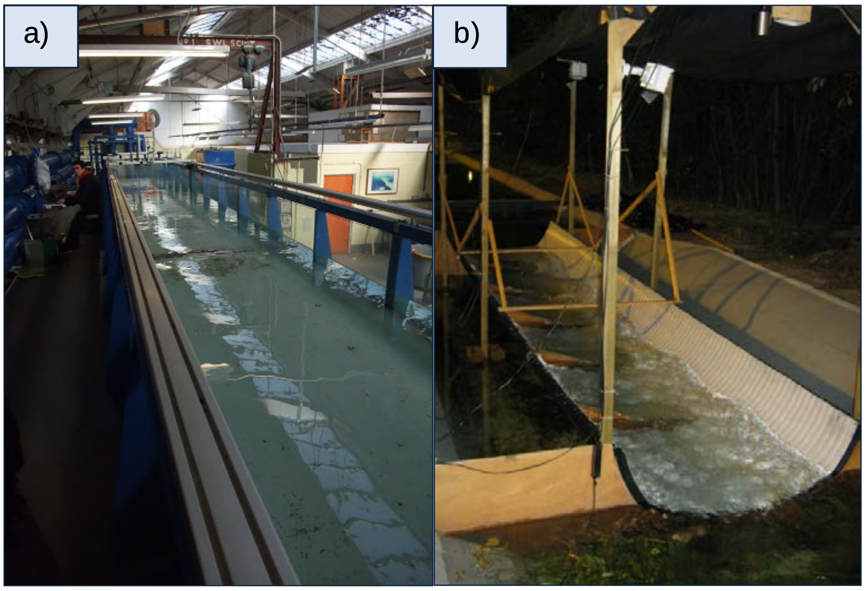


Plate 4.4. Large open channel flume facilities at the International Centre for Ecohydraulics Research laboratory facilities, University of Southampton, UK: a) indoor rectangular flume; and b) outdoor trapezoidal flume fitted with a full scale culvert and prototype baffle design.

4.6. Fish Behaviour

Trials were filmed using between one and four lateral or overhead video cameras for subsequent analysis of fish behaviour. Cyprinid trials were completed during daylight, with the flume evenly lit using overhead lights, as both common and bighead carp have been found to be diurnally active (Crook, 2004; Peters *et al.*, 2006; Baumgartner *et al.*, 2008). All experimental studies on European eel were completed during hours of darkness to replicate their predominantly nocturnal migrations (Tesch, 2003; Travade *et al.*, 2010). This also removed visual cues, thus enhancing confidence that behaviour was induced by the hydraulic conditions (behavioural response due to physical contact with a structure could be observed and accounted for). Infrared lights (850 nm) and cameras were used to film eel trials as this is beyond their visual spectrum (Carlisle and Denton, 1959).

Fish behaviour was quantified either by: 1) assigning fish to categories of behaviour (e.g. rheotactic orientation, utilisation of low velocity areas, reaction to a hydraulic stimulus) (Fig. 4.2a); 2) recording count variables such as approach or attempt rate; or 3) by tracking fish movements (Fig. 4.2b). Tracking was conducted manually using Vernier Logger Pro 3.8.2 (Vernier Software & Technology, Oregon, USA) to locate the fish's snout and digitise the co-ordinates. Fish locations, were adjusted for the 'fish eye effect' and their positions relative to the experimental area were imported into ArcGIS v. 9.3 (ESRI, Redlands, USA), where the hydraulic conditions experienced could be extracted from other data layers.

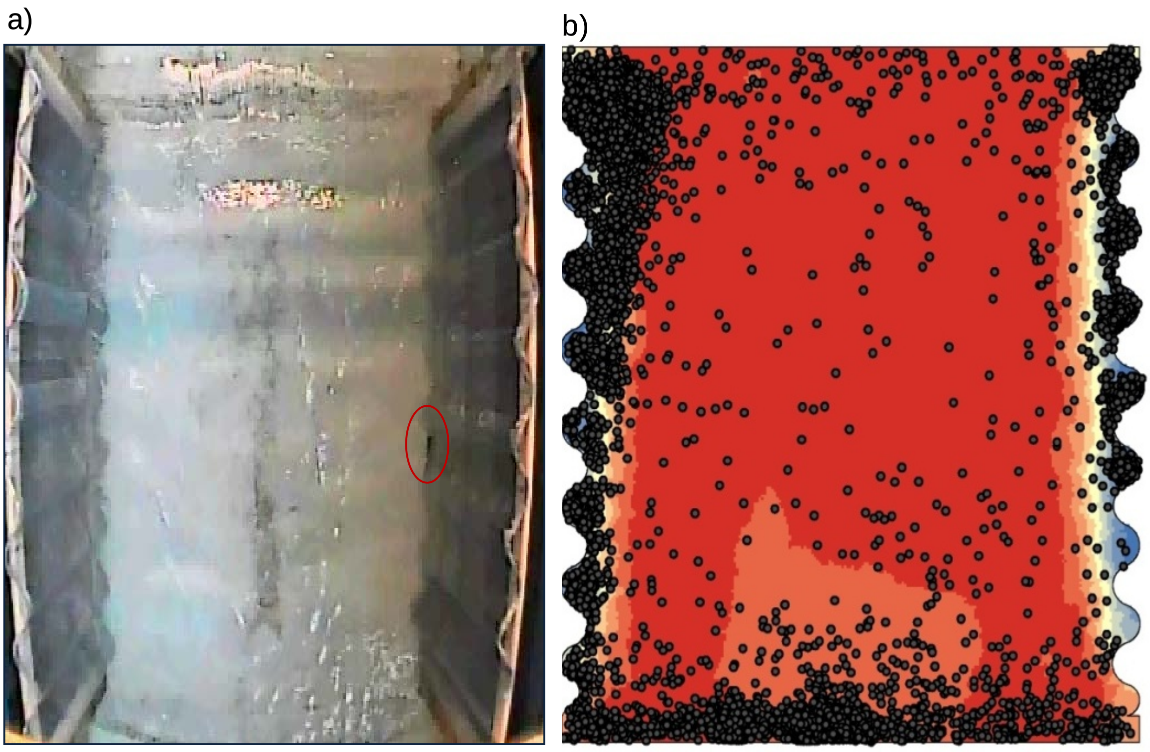


Figure 4.2. Evaluation of common carp swimming behaviour under various wall roughness treatments: a) behaviour could be categorised based on whether individuals utilised the area of low velocity within corrugation troughs, as demonstrated by the fish circled in red; and b) each individual's head position was tracked every 1 second and overlaid onto a hydraulic profile of the flume (velocity = 0.16-0.58 m s^{1}) in ArcGIS to extract the conditions experienced.

4.7. Flume hydraulics

The hydraulic conditions within experimental areas were measured after biological trials along transects perpendicular to flow. The location and density of sample points were dependent on the complexity of flow conditions, fish length, and the locations predominantly occupied. Maximum sampling density was every 2 cm if small fish occupied areas of rapidly changing hydraulic conditions. Velocity was recorded at 60% depth as a measure of mean channel conditions (Hooper and Kohler, 2000), and in some studies 2 cm above the channel floor as an indicator of what is likely experienced by bottom swimming fish. Velocity was recorded using either a propeller flow meter (NTK71-Vectrino, Qingdao Nortek Measuring Equipment Co., Qingdao, China), electromagnetic flow meter (Model 801, Valeport, Totness, UK), or an Acoustic

Doppler Velocimeter (ADV; Nortek+, Nortek AS, Oslo, Norway). The propeller and electromagnetic flow meters were utilised when analysis of turbulence was not necessary, or when water was too shallow to utilise an ADV.

ADVs use the Doppler shift principle; sound pulses are emitted from the probe and reflected back from particles in the water to the sensor. The frequency shift between the transmitted pulse and received echo is proportional to the speed of suspended particles, which is assumed to be equal to water velocity. Using an ADV allows the collection of large quantities of data in three dimensions (longitudinal, lateral and vertical), without interfering with flow conditions as the sampling area is at least 5 cm below the probe tip (Nikora and Goring, 1998). ADV data were collected using a sample volume of 3.1 mm, at 50 Hz, for 60 or 90 seconds, to create a dataset of 3000 or 4500 velocity measurements in each plane. The signal to noise ratio was approximately 20 and the correlation coefficient was generally over 70%, as recommended by the manufacturer to indicate high signal strength and reliable data.

Errors within raw ADV data are apparent as erroneous spikes not correlated to the majority of points, which result in the calculated intensity of turbulence being greater than reality (Garcia *et al.,* 2005; Cea *et al.,* 2007). Such spikes were detected, removed, and replaced by a maximum / minimum threshold or velocity correlation filter, in Microsoft Office Excel 2010 (methods fully described by Cea *et al.*, 2007). Maximum / minimum thresholds were calculated as:

$$u_{min} = \bar{u} - \sqrt{2\ln(n)}\ \sigma_u \tag{4.1}$$

$$u_{max} = \bar{u} + \sqrt{2\ln(n)}\ \sigma_u \tag{4.2}$$

where $u_{min}/_{\max}$ are the longitudinal velocity thresholds, $\bar{u}$ is the mean longitudinal velocity, σ_u is the standard deviation of u, and n is the number of data points. In Chapter 6, a velocity correlation filter was applied; velocity fluctuations about the mean in all three dimensions are plotted against each other and it is assumed that valid data cluster inside an ellipsoid, thus filtering the combined dimensions rather than treating each independently. Both filters removed data outside of the thresholds and replaced them with the mean sample value.

The filtered data were used to study velocity in each plane and to calculate the mean velocity vector:

$$U = \sqrt{u^2 + v^2 + w^2} \tag{4.3}$$

where u, v and w are the longitudinal, horizontal and vertical components of flow, respectively.

The turbulent kinetic energy was calculated as it provides a dimensional value for the order of magnitude of turbulence. It is a measure of the energy extracted from the mean flow by the motion of turbulent eddies (Bradshaw, 1971) and is calculated as:

$$TKE\ (\mathrm{J\ m^{-3}}) = 0.5\,.\,\rho\,.\,(\sigma_u^2 + \sigma_v^2 + \sigma_w^2) \tag{4.4}$$

where ρ is the density of water (1000 kg m^{-3}). The relative turbulence intensity was also calculated ($TI = \sigma_u/U$) and explored in preliminary analysis. However, normalising the intensity of turbulence by mean velocity can result in similar *TI* values between treatments with different turbulence magnitudes, and it is difficult for the reader to determine the actual hydraulic conditions experienced by fish (Lacey *et al.*, 2011). It has therefore been recommended that studies report dimensional metrics (e.g. Reynolds shear stresses, TKE and vorticity) so that comparisons can be made with other laboratory and field studies (Lacey *et al.*, 2011). The point longitudinal velocity, or *U*, and TKE data were plotted and interpolated in ArcGIS.

Chapter 5: Swimming performance and behaviour of bighead carp (*Hypophthalmichthys nobilis*): application to fish passage and exclusion criteria

5.1. Abstract

The bighead carp (*Hypophthalmichthys nobilis*, Richardson 1845) is one of the most commercially important freshwater fish species in China, but their abundance has declined considerably in recent decades, partly due to river regulation. In other countries it is invasive, posing an ecological and economic threat. To improve fish pass effectiveness at impediments to migration in its native range, and create velocity barriers to reduce range expansion where it is invasive, an improved understanding of swimming ability and behaviour is needed. The burst, prolonged, and sustained swimming performance of juvenile bighead carp were quantified experimentally through constant acceleration trials (U_{max}), fixed velocity tests, and volitional passage efficiency tests for three consecutive constrictions. The effect of length, temperature, swimming speed and method (swim chamber / open channel flume section) on endurance was evaluated for fixed velocity trials. The utilisation of low velocity areas close to the flume edge and floor at different mid channel velocities was explored. Based on endurance data, the maximum sustained swimming speed reported was 5.81 $FL\ s^{-1}$ (mean = 3.84 $FL\ s^{-1}$), and burst speeds reached 12.78 $FL\ s^{-1}$ (mean = 7.80 $FL\ s^{-1}$). The mean (± S.E.) U_{max} was 6.81 (± 0.45) $FL\ s^{-1}$. Method did not influence endurance in the fixed velocity trials and fish rarely utilised low velocity areas in the corners of the flume when mid channel velocity exceeded sustained swimming ability. The variability in behaviour may have been due to turbulence causing instability in swimming posture. Passage efficiency decreased at successive flume constrictions, possibly indicating a poor repeat burst performance. It is recommended that for bighead carp 50 to 100 mm long, velocities should not exceed 0.60 m s^{-1} where burst swimming is needed to pass short velocity barriers and areas below 0.40 m s^{-1} should be available in fish pass pools, with regular resting points provided in long fish passes. To reduce the spread of invasive fish up to 200 mm long, maintenance of velocities greater than 1.3 m s^{-1} over 50 m is likely to impede movement at temperatures similar to those presented in this

study (18 - 27 °C). Field validation is required to verify wild bighead carp behaviour and passage in the hydraulic conditions created by fish passes.

5.2. Introduction

Bighead carp (*Hypophthalmichthys nobilis*, Richardson 1845), silver carp (*H. molitrix*, Valenciennes 1844), grass carp (*Ctenopharyngodon idella*, Valenciennes 1844) and black carp (*Mylopharyngodon piceus*, Richardson 1846) (herein collectively referred to as Asian carp) are the most commercially important freshwater fish species in China, particularly in the Yangtze River basin. They contributed 60% to China's freshwater fisheries catch in the 20th century (Wu *et al*., 1992) and 80 to 90% of the mid Yangtze River catch in the 1960s (Chen *et al.*, 2004). Although commercial harvest continues, recruitment and catch has declined considerably (Liu *et al*., 2004; Duan *et al*., 2009; Yi *et al*., 2010), contributing only 0.52 to 5% of the mid Yangtze catch in the 1990s (Chen *et al.*, 2004). The decline in recruitment is likely a result of numerous pressures, including overfishing, pollution, land reclamation, and construction of dams and sluice gates (Xie and Chen 1999; Fu *et al*., 2003; Yi *et al*., 2010). Impoundments have flooded spawning grounds, altered flow and temperature regimes, and caused longitudinal and lateral habitat fragmentation (Wei *et al*., 1997; Duan *et al*., 2009; Zhang *et al*., 2012). Larval abundance of the major carp at Sanzhou on the Yangtze River decreased from between 1.9 and 3.6 billion between 1997 and 2002, to 0.34 billion in 2004 and 0.11 billion in 2005, following flooding of spawning grounds due to the construction of the Three Gorges Dam (Duan *et al.*, 2009). After spawning the eggs and larvae drift downstream and juveniles move to side channel habitat and lakes for growth (Jennings, 1988; Zhang *et al*., 2012). This lateral migration has been restricted by widespread sluice gate installation for water conservation projects and all lakes, except Dongting and Poyang, have been isolated from the main Yangtze River channel (Fu *et al*., 2003; Chen *et al*., 2004). Sluice gates proposed for Poyang Lake outlet further threaten the sustainability of these potamodromous fish, unless effective mitigation is provided (Finlayson *et al*., 2010).

Fish passes are increasingly recommended at new barriers in China to mitigate for impeded migration (Finlayson *et al*., 2010; Zheng *et al*., 2010). Evaluation of their efficiency is rare (see Zhili *et al*., 1990 for exception), but anecdotal evidence suggests many old structures are ineffective because they are based on Western designs not developed for Asian species (Dudgeon, 1995; Fu *et al*., 2003; Dudgeon, 2005; Zheng *et al*., 2010). To adapt designs to native fish there is a need to improve understanding of the target species' swimming performance and behaviour (Clay, 1995; Larinier, 2002b; Katopodis, 2005). Performance data help determine suitable velocity criteria, and in turn define optimal pass dimensions, slope, and frequency of resting pools (Clay 1995; Rodríguez *et al*., 2006), while understanding behavioural response to hydraulic stimuli can improve attraction and passage efficiency (e.g. Silva *et al*., 2009; Piper *et al*., 2012; Vowles and Kemp, 2012). For the majority of Chinese fish species quantification of swimming performance is limited and behaviour in non-uniform flow unexplored (Chapter 2).

The four Asian carp species have been introduced to many countries for biological control and aquaculture, and have had a negative impact on many native species and ecosystems (Lehtonen, 2002; Nico *et al.*, 2005; Wittmann *et al.*, 2014). For example, invasive silver and bighead carp became established in the U.S. in the 1980s (Kolar *et al*., 2005; Conover *et al*., 2007). They can outcompete native species due to their fast growth rate and efficient filter feeding, and are linked to a decline in body condition of native gizzard shad (*Dorosoma cepedianum,* Lesueur 1818) and bigmouth buffalo (*Ictiobus cyprinellus*, Valenciennes 1844) (Irons *et al*., 2007; Sampson *et al*., 2009). In addition, high densities of silver carp leaping from the water can damage boats and harm anglers (Stokstad, 2010). In response to the threat to native species and the recreational fishing industry, federal agencies released $75.8 million in 2010 for control and research to prevent further spread of silver and bighead carp, particularly to the Laurentian Great Lakes (Stokstad, 2010; ACRCC, 2012). Hydraulic barriers that constrict the channel to elevate velocity above the swimming ability of the target species are a potential method for reducing the spread of invasive fish (Hoover *et al*., 2003; Neary *et al*., 2012; Noatch and Suski, 2012), including Asian carp.

Fish swimming speeds are commonly categorised based on endurance time as: 1) sustained, which can be maintained indefinitely by aerobic metabolism; 2) burst, which is powered by anaerobic metabolism lasting less than 20 s; and 3) prolonged, which combines aerobic and anaerobic metabolism to fuel swimming for between 20 s and 200 min (Brett, 1964; Brett *et al*., 1958; Beamish, 1978). Fish swimming performance is commonly quantified using swim chambers, permitting accurate velocity and temperature control (Hammer, 1995). However, the confined conditions in which fish are forced to swim prevent exhibition of natural performance enhancing behaviours, such as burst-and-coast swimming (Peake and Farrell, 2004; Tudorache *et al*., 2007). Cessation of swimming in chamber based performance tests may reflect a behavioural response to the unnatural conditions, rather than physiological exhaustion, and recent volitional flume studies have revealed higher than predicted (based on the results of swim chamber tests) burst swimming speeds for several species (Mallen-Cooper, 1994; Peake, 2004a; Peake and Farrell, 2006; Holthe *et al*., 2009; Russon and Kemp, 2011a). Furthermore, the uniform flows created within swim chambers prevent utilisation of low velocity areas commonly available under more hydraulically diverse natural conditions. It is assumed that fish use areas of low velocity to minimise the energetic cost of upstream movements, and that this behaviour can enable small and weak swimming fish to pass man-made structures even when the average bulk flow exceeds swimming ability (House *et al*. 2005; Richmond *et al*., 2007). Attempts to verify this assumption through behavioural observation are uncommon (Katopodis, 2005).

This study focused on bighead carp as a model species to improve the understanding of Asian carp swimming ability. Reliable data for bighead carp performance are presented in one recent report on endurance (Hoover *et al*., 2012), while previous in situ and laboratory studies are based on few replicates and poorly defined performance criteria (Zhao and Han, 1980; Layher and Ralston, 1997). The data obtained will aid efforts to design more effective fish passes within the native range, and may help to reduce their spread through the development of velocity barriers where they are invasive.

The primary aim of this study was to quantify the sustained, prolonged, and burst swimming speeds of juvenile bighead carp, a critical life stage during which migration to lakes occur. This aim was achieved through: i) fixed velocity trials in a swim chamber and section of open channel flume to quantify performance in all three swimming modes; ii) a constant acceleration test to evaluate anaerobic capacity; and iii) evaluation of repeat burst performance during volitional passage through three consecutive channel constrictions. A secondary aim was to evaluate bighead carp behaviour and its influence on performance, by comparing: a) the utilisation of low velocity areas in the flume under various flow conditions and endurance during swim chamber and flume based fixed velocity tests; and b) passage predictions based on forced swimming tests with those obtained during volitional swimming through the channel constrictions. It was hypothesised that: 1) fish would utilise the low velocity areas of the flume during fixed velocity tests, therefore performance would be better in the flume that swim chamber; and 2) volitional passage of the constrictions would be better than predicted from forced swimming performance tests.

5.3. Methods

5.3.1. Fish maintenance

Experiments were conducted during two experimental periods in 2010 and 2011.

In May and June 2010, 120 bighead carp (mean ± S.E. fork length [*FL*] = 181 ± 37 mm, mass = 114.3 ± 5.5 g) were net caught at Longquan aquaculture pond, Jiangxia District, and transported 3 h in aerated bags to the Institute of Hydroecology, Ministry of Water Resources, Wuhan, China (30° 30’ 17.01”N, 114° 22’ 36.04”E). Fish were held in two 1430 L outdoor tanks sterilised with potassium permanganate to minimise the risk of disease. Constant water exchange with an adjacent large fish pond was used to stabilise water temperature (mean ± S.E. = 23.8 ± 2.1 °C).

In April and May 2011, 184 bighead carp (mean ± S.E. *FL* = 103 ± 30 mm, mass = 28.5 ± 2.3 g) were transported 2 h in aerated bags from the Dangyang hatchery to the China Three Gorges University, Yichang (30° 43’ 47.38”N, 111° 18’ 26.04”E). A 5300 L filtered and aerated outdoor tank was used to hold fish at a mean (± S.E.) temperature of 19.5 (± 3.4) °C.

During both experimental periods water quality was monitored daily and partial water changes conducted weekly to ensure low nitrate (< 50 mg L^{-1}) and nitrite (< 1 mg L^{-1}) concentrations. Fish were fed daily and all trials were conducted between 3 and 14 days after fish were delivered to experimental facilities. Test facilities were maintained at water temperatures (18-27°C) representative of those found in the Yangtze River during juvenile migrations (H. Maolin, per. com.), and within the preferred range for bighead carp spawning and feeding (Jennings, 1988). After trials, fish were anaesthetised in tricaine methanesulfonate (MS-222), weighed (grammes) and measured (*FL:* mm).

5.3.2. Swimming performance during fixed velocity tests

Fixed velocity tests were conducted using a swim chamber at the China Three Gorges University between 6 and 13 April 2011 (n = 145, FL = 52 - 190 mm) and a section of open channel outdoor flume at the Institute of Hydroecology between 5 May and 26 June 2010 (n = 120, FL = 123 - 251 mm).

Flow was driven through the centre of a 93 L Steffensen type swim chamber (Steffensen *et al.*, 1984) by a three phase electric motor and returned through two test sections (0.80 m long, 0.15 m wide and 0.15 m deep) on opposite sides. Temperature (mean ± S.E. = 21.5 ± 0.2 °C) was controlled by constant water exchange with an aerated and regulated buffer tank. A cross vane baffle and flow straightener homogenised flow conditions. Homogeneous swim chamber velocity conditions permit the assumption that fish swimming speed is equal to mid channel water velocity (Nikora *et al.*, 2003). The linear relationship between motor frequency and velocity (calibrated using an impeller flow meter: NTK71-Vectrino, Qingdao Nortek Measuring Equipment Co., Qingdao) was used to determine test water velocity, which had a maximum of 0.82 m s^{-1}. The cross-sectional area of the largest fish was less than 10% of that of the channel. Therefore, increased water velocity due to partial blocking of the flow by the fish was deemed negligible, and following standard practice (e.g. Bell and Tehrune, 1970) no adjustment to swimming speeds was made.

A re-circulatory open channel flume (13 m long, 0.6 m wide and 0.8 m deep) was used for trials in heterogeneous flow conditions, within a central 1 m long test section created using 15 mm square mesh screens. Mean (± S.E.) water temperature was 22.4 (± 0.2) °C. A honeycomb flow straightener was installed at the inlet. Water velocity was controlled by three (5.5, 7.5 and 18.5 KW) pumps to adjust discharge and an outlet weir to regulate water depth. Mid-channel velocity and depth ranged from 0.38 to 1.25 m s^{-1} and 0.20 to 0.36 m, respectively. For initial analysis, swimming speed was considered equal to mid channel velocity (V_{mid}), which was recorded at 60% water depth after each trial.

Individual fish were tested once under a single velocity. Following 1 h acclimatisation at approximately 1 FL s^{-1} (within known sustained speeds, Hoover *et al.*, 2012), velocity was increased to the test level within 1 min and 1 - 2 min in the swim chamber and flume section, respectively. Test velocities were within the sustained to burst swimming speed range but varied between the chamber and flume due to differences in the subjects *FL* and the equipment's maximum capacity (Table 5.1). Resting on the downstream screen was discouraged by gently tapping the glass or caudal fin. Individuals were classified as swimming at burst, prolonged, or sustained speeds based on endurance (Beamish, 1978), defined as the time interval between reaching the test velocity and impingement on the downstream screen for 3 s. In the flume, trials were ended after 200 min whereby it was assumed fish were swimming at a sustained speed (methods reviewed in: Hammer, 1995). The maximum trial length was reduced to 120 min during the swim chamber tests as pilot experiments and data from the flume study indicated no fatigue occurred after this period.

Table 5.1. The number and fork length (*FL*) of bighead carp (*Hypophthalmichthys nobilis*) tested over a range of water velocities during fixed velocity tests in a section of open channel flume and swim chamber. Water velocity was measured at 60% depth in the centre of the test section. Maximum water velocity was limited to 0.82 m s^{-1} in the swim chamber. The maximum velocity tested in the flume was 1.25 m s^{-1}, as beyond this the test subjects could not maintain active swimming.

Water velocity	**Swim chamber**		**Flume section**	
(m s^{-1})	**frequency**	***FL***	**frequency**	***FL***
0.36 - 0.45	12	0.08 - 0.11	9	0.10 - 0.14
0.46 - 0.55	41	0.06 - 0.18	12	0.10 - 0.17
0.56 - 0.65	40	0.06 - 0.17	14	0.11 - 0.22
0.66 - 0.75	40	0.06 - 0.18	26	0.14 - 0.23
0.76 - 0.85	12	0.11 - 0.19	18	0.15 - 0.25
0.86 - 0.95	0	na	12	0.14 - 0.21
0.96 - 1.05	0	na	10	0.16 - 0.25
1.06 - 1.15	0	na	8	0.18 - 0.25
1.16 - 1.25	0	na	11	0.15 - 0.24
Total fish	**145**	**0.06-0.19**	**120**	**0.10-0.25**

The combined (swim chamber and flume) data were divided into the three swimming speed modes. The relationship between swimming speed (*U* [*FL* s^{-1}]), water temperature

(T [°C]), method (M: flume section or swim chamber), and endurance was assessed using linear regression. The maximum sustained swimming speed (U_S) model was:

$$U_S = b_0 + b_1T + b_2FL + b_3M \tag{5.1}$$

where b_i are the regression coefficients. This equation was used to predict the mean (± 90% C.I.) of the maximum sustained speed for fish of a known *FL*, at a specific temperature. For prolonged swimming speeds there was insufficient data to construct an accurate model for endurance times that exceeded 10 min. Therefore, only individuals swimming for between 20 s and 10 min were included in the prolonged swimming speed (U_P) regression analysis (Equation 5.2) and those with endurance less than 20 s in the burst analysis (U_B) (Equation 5.3):

$$\ln(E) = b_0 + b_1U_P + b_2T + b_3M \tag{5.2}$$

$$\ln(E) = b_0 + b_1U_B + b_2T + b_3M \tag{5.3}$$

5.3.3. Constant acceleration test

The maximum swimming speed ($U_{max;}$ e.g. Farrell, 2008) of bighead carp, a measure of anaerobic performance, was calculated for 10 individuals using a constant acceleration test. Trials were conducted in the swim chamber described for fixed velocity tests, at the China Three Gorges University, on 15 April 2011. After 1 h acclimatisation at 1 FL s^{-1}, velocity was increased by 0.02 m s^{-1} every minute until fatigue to determine the U_{max}. Water temperature was 23.1 °C during all trials. Fish were selected to minimise variation in *FL* (mean ± S.E. = 76.4 ± 2.3 mm) and correlation between individual U_{max} and *FL* was assessed using Spearman’s rank correlation (R_s). The mean U_{max} was compared to the predicted sustained speed for 76 mm fish using the results of equation 5.1 and the predicted endurance at U_{max} based on equation 5.2.

5.3.4. Swimming behaviour during fixed velocity tests

A sub-sample (n = 64) of the flume based fixed velocity tests were filmed to enable detailed analysis of swimming behaviour. Following each trial the velocity 0.02 m from the wall and floor ($V_{refugia}$) was recorded using an impeller flow meter and compared to V_{mid} (Fig. 5.1). The length of time spent *utilising flow refugia* (holding station in low velocity areas close to the flume wall and floor) was recorded and subtracted from the total trial duration, and the difference deemed to be allocated to *free swimming*. The relationship between percentage of time spent utilising flow refugia and free swimming, relative to fish length, was explored using Spearman's rank correlation. Swimming speeds were corrected (U_{cor}) for the time spent utilising flow refugia by:

$$U_{\mathrm{cor}} = (\, t_1 \times V_{\mathrm{refuge}}) + (\, t_2 \times V_{\mathrm{mid}}) \tag{5.4}$$

where t_1 and t_2 are the proportion of time spent utilising flow refugia and free swimming, respectively.

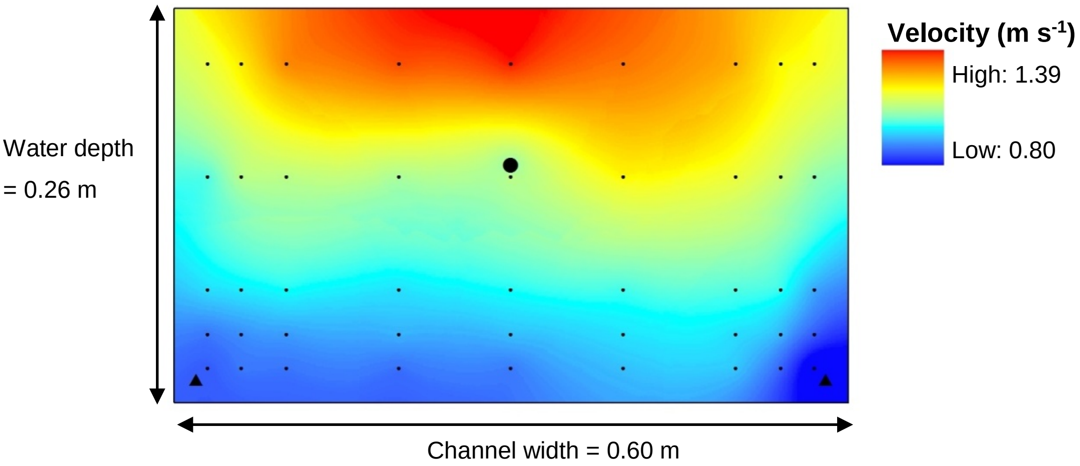


Figure 5.1. Velocity cross-section (viewed looking upstream) of the flume section used to assess the swimming performance of bighead carp (*Hypophthalmichthys nobilis*) in fixed velocity tests. Longitudinal velocity was measured using an impeller flow meter at each sample location (small dots) and interpolated using spline methods in ArcGIS. The velocities at 60% of water depth in the test section centre (V_{mid}: large dot) and 0.02 m from walls and floor (V_{refugia}: triangles) were recorded after each trial. In this example V_{mid} was 1.08 m s^{-1} and V_{refugia} approximately 0.8 m s^{-1}.

5.3.5. Volitional burst swimming performance and behaviour

To evaluate the volitional repeat burst swimming performance of bighead carp, passage efficiencies at three consecutive constrictions (vertical slots) were evaluated in a 4.5 m long test section of an open channel, oval, recirculating raceway (6.50 m long, 0.37 m wide, 0.70 m deep), at the China Three Gorges University. Trials were conducted on the

18 and 19 May 2011. Four electrically powered, in channel, centrifugal pumps, controlled the velocity while depth remained constant at 0.22 m. Honeycomb flow straighteners delineated the 4.5 m test section, which began 1.4 m downstream of the first constriction approached by upstream moving fish. Constrictions, created from 3 mm width Plexiglass panels, reduced the flume width to 0.14 m, and divided the test area into three sections, including two low velocity pools (1.15 m and 1.25 m long; Fig. 5.2). Trials were conducted under two velocity treatments (maximum velocity = 0.50 m s^{-1} and 0.57 m s^{-1} for low and high treatments, respectively; Fig. 5.2) by altering the number of pumps in use. Based on the endurance and U_{max} results it was predicted that anaerobic swimming would be required to pass the velocities encountered downstream of the constrictions, but that passage would be possible. An Acoustic Doppler Velocimeter (ADV; Nortek +, Nortek AS, Oslo, Norway) was used to measure mean longitudinal velocity at 60% water depth, sampling at 50 Hz for 60 s (sample locations shown in Fig. 5.2). Data spikes were removed using a maximum / minimum threshold filter (Cea *et al.*, 2007) prior to interpolation in ArcGIS.

Individual fish (n = 29, mean ± S.E. *FL* = 101.0 ± 1.7 mm) were allowed at least 1 h to acclimatise to flume conditions in a perforated container downstream of the test section (mean ± S.E. temperature = 25.3 ± 0.1 °C) before release at the downstream screen. Trials ended after successful upstream exit through the three constrictions (whole body passed upstream of the final constriction = success) or after 30 min. Three cameras (1.5 m above the channel floor) recorded behaviour.

The number of approaches to constriction 1 (movement into the high velocity area 0.05 m downstream; Fig. 5.2) was recorded and converted to a rate dependent on the time available to individuals before ascent. The effect of velocity treatment on approach rate was evaluated using an exact Mann-Whitney test. The number of passes at each constriction was recorded for each individual. Passage efficiency was calculated as the percentage of the total fish tested that successfully moved upstream of each constriction. Exact Mann-Whitney tests were used to evaluate the effect of *FL*, mass, and water temperature on success.

Qualitative observations of swimming behaviour in terms of swimming gait, depth in the water column, and utilisation of high and low velocity areas were recorded. All statistical analysis was completed in IBM Statistics v. 19 (IBM Corp, Armonk, USA).

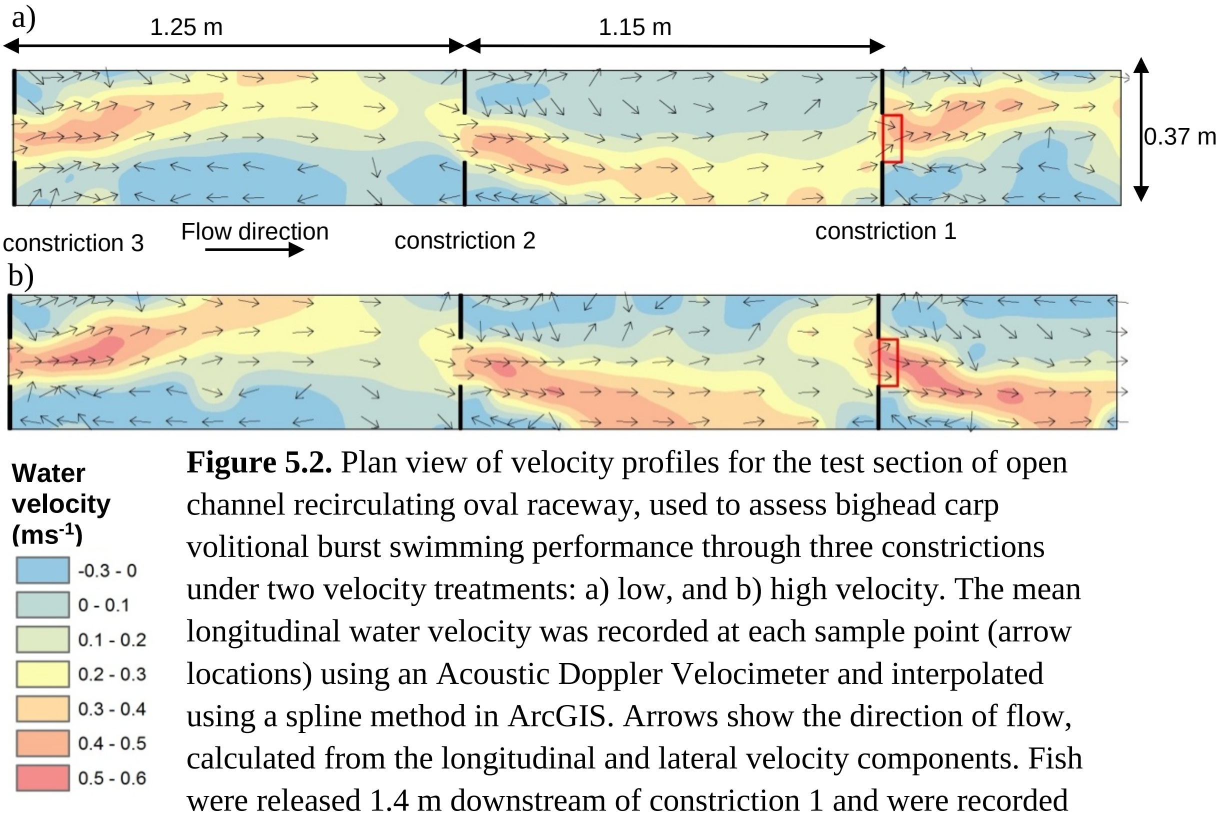


Figure 5.2. Plan view of velocity profiles for the test section of open channel recirculating oval raceway, used to assess bighead carp volitional burst swimming performance through three constrictions under two velocity treatments: a) low, and b) high velocity. The mean longitudinal water velocity was recorded at each sample point (arrow locations) using an Acoustic Doppler Velocimeter and interpolated using a spline method in ArcGIS. Arrows show the direction of flow, calculated from the longitudinal and lateral velocity components. Fish were released 1.4 m downstream of constriction 1 and were recorded as approaching when they reached 0.05 m downstream (area outlined in red).

5.4. Results

5.4.1. Swimming performance during fixed velocity tests

The mean (± S.E.) sustained swimming speed for bighead carp was 3.84 ± 0.12 *FL* s^{-1} (equivalent to 0.37 – 0.78 m s^{-1}). As method had no effect on sustained speeds ($t = -1.08$, $P = 0.29$) it was excluded from further regression analysis. Maximum sustained swimming speed was positively related to both *FL* and temperature (Equation 5.5; $R^2 = 0.72$, $F_{2,46} = 58.41$, $P < 0.001$):

$$U_S = -0.268 + (0.026 \times T) + (1.640 \times FL) \tag{5.5}$$

Endurance was low when water velocity exceeded sustained swimming ability in both the flume section and swim chamber, with only 12 fish able to swim for longer than 10 min. Prolonged swimming speeds (endurance > 20 s < 10 min) ranged from 2.43 to

11.31 FL s^{-1} (equivalent to 0.30 to 1.23 m s^{-1}). Neither temperature nor method had an effect on endurance at prolonged swimming speeds (T: $t = -0.11$, $P = 0.91$, M: $t = 0.70$, $P = 0.49$) and were excluded from regression analysis. Endurance was negatively related to swimming speed, but with high variability (Equation 5.6; $R^2 = 0.26$, $F_{1,155} = 54.70$, $P < 0.001$):

$$lnE \ = 1.74 - \ (0.24 \times U_P) \tag{5.6}$$

Burst swimming speeds (endurance < 20 s) ranged from 3.41 to 12.78 FL s^{-1} (equivalent to 0.41- 1.22 m s^{-1}), with a mean (± S.E.) of 7.80 ± 0.41 FL s^{-1}. Burst swimming speeds within the section of open channel flume were variable and there was no relationship between velocity and endurance ($F_{2,14} = 2.33$, $P = 0.13$), therefore, only swim chamber data were analysed. Here, endurance was not influenced by temperature ($t = 0.78$, $P = 0.44$), and although it was negatively related to swimming speed, the relationship was still highly variable (Equation 5.7; $R^2 = 0.20$, $F_{2,29} = 6.69$, $P = 0.04$):

$$lnE \ = -0.90 - \ (0.08 \times U_B) \tag{5.7}$$

5.4.3. Constant acceleration test

There was no correlation between $U_{\max}$ and FL over the small size range tested ($R_s = -0.35$, $P = 0.32$). The mean (± S.E.) $U_{\max}$ was 6.81 (± 0.45) FL s^{-1} (equivalent to 0.51 m s^{-1}). Using equation 5.5 for a 76 mm long fish at 23 °C, the predicted mean sustained speed was 5.9 FL s^{-1} (0.45 m s^{-1}). Due to large variation between individuals in the fixed velocity trials, the $U_{\max}$ was within both the burst and prolonged swimming speed range for 60 to 90 mm fish, although it was exceeded by 90% of individuals swimming at burst speeds. Endurance at this speed for fish swimming in the prolonged mode was estimated as 67 s.

5.4.4 Swimming behaviour during fixed velocity tests

The V_{refugia} was up to 40% lower than V_{mid}. The proportion of time fish spent utilising flow refugia was negatively correlated to V_{mid} ($n = 64$, $R_s = 0.42$, $P < 0.001$, Fig. 5.3). Of the 18 fish swimming at a sustained speed, 11 spent over 50% of the time utilising flow refugia, compared to only 2 of the 46 fish swimming at burst or prolonged speeds. By estimating average swimming speed based on the time spent utilising flow refuging behaviour, the mean sustained and prolonged speeds were respectively 3.31 and 4.79 *FL* s^{-1}, compared to 3.67 and 4.82 *FL* s^{-1} when assuming swimming speed was equal to V_{mid}.

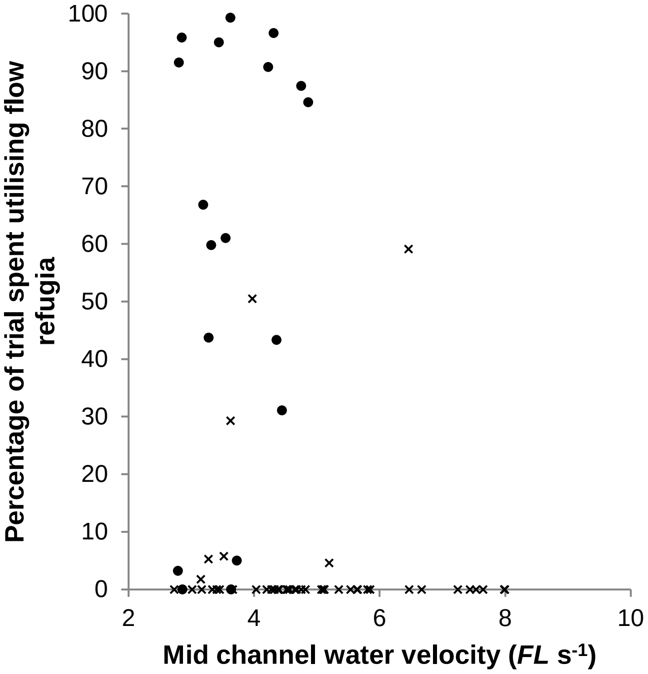


Figure 5.3. Relationship between mid-channel flume velocity (V_{mid}) and the percentage of trial time individual bighead carp spent utilising flow refugia near the flume wall and floor. Data was split into fish swimming at sustained (solid circles) and prolonged or burst (crosses) speeds.

5.4.5. Volitional burst swimming performance and behaviour

All fish approached constriction 1 (Fig. 5.2) and there was no effect of treatment on approach rate (Mann-Whitney $U = 94$, $P = 0.64$). Fish passed constriction 1 up to eight times under both velocity treatments and constriction 2 a maximum of two and four times under the high and low treatments, respectively. Passage efficiency decreased from 87 and 100% at constriction 1, to 67 and 71% at constriction 3, under the high and low velocity treatments, respectively (Fig. 5.4). Under the high velocity treatment, successful fish had a greater length and mass (median = 98 mm and 16.5 g) than those that failed (94 mm, 14.7 g) (*FL,* $U = 8$, $P = 0.04$; mass, $U = 6$, $P = 0.02$). There was no difference under low velocity (*P* > 0.05). There was no effect of water temperature during either treatment (*P* > 0.05).

Fish swam close to the channel floor throughout the trials. Individuals tended to utilise low velocity areas between passing the constrictions, but moved into the channel centre where velocity was highest on approach (Fig. 5.2). Although an unsteady gait was occasionally observed for some fish in lower velocity areas, all maintained high speed steady swimming to pass the constrictions.

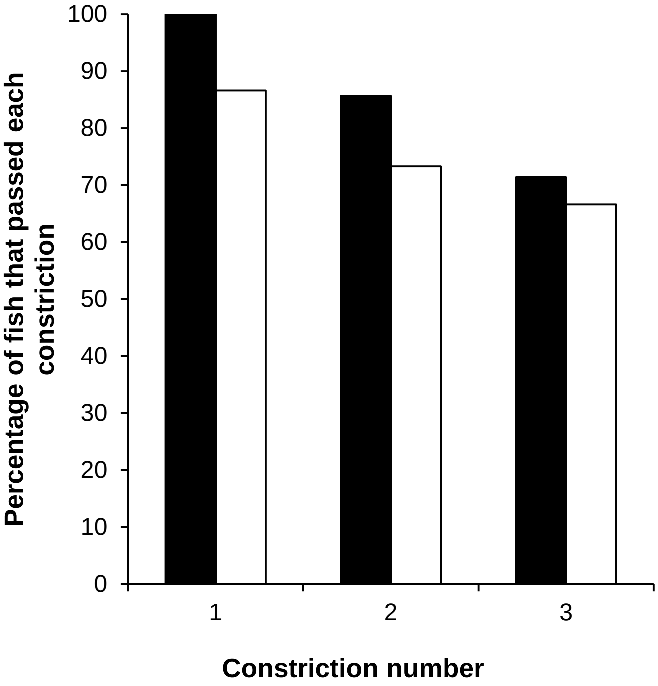


Figure 5.4. The passage efficiency of bighead carp (% of total tested fish) at three consecutive vertical slot constrictions in an open channel flume at the China Three Gorges University, under high (solid bar, *n* = 15) and low (clear bar, *n* = 14) velocity treatments. Constrictions numbered from most downstream (1) to upstream (3).

5.5. Discussion

Loss of connectivity between essential freshwater habitats, due to the construction of anthropogenic structures such as dams, is one of the key causes of Asian carp population decline (Yi *et al.*, 2010). Fish passes provide an important means to mitigate for this environmental impact, but designs must be based on understanding the swimming ability and behaviour of the target species or guilds (Zheng *et al.*, 2010). By using a variety of methods, this study enhanced understanding of juvenile bighead carp swimming performance and provided the first data on behaviour. This may be used to inform fish passage design for Asian carp in China, and potential development of velocity barriers in regions where they are invasive.

The use of multiple methodologies to quantify fish swimming performance and behaviour enhances confidence in the accuracy of results and application to fisheries management (Bestgen *et al.*, 2003). As anaerobic metabolism likely contributed to swimming during a number of the one minute velocity increments during the constant acceleration tests, and the total protocol lasted approximately 20 min, it is likely that U_{max} described prolonged rather than burst swimming ability. The juvenile bighead carp U_{max} (mean = 0.51 m s^{-1}) was comparable to speeds that equal sized fish (76 mm) could maintain for approximately one minute in the fixed velocity test. Burst speeds for 50 to 120 mm length fish ranged from 0.45 to 0.82 m s^{-1}, and some fish failed to ascend the flume constrictions (Fig. 5.4), which required swimming at speeds in excess of 0.5 to 0.57 m s^{-1} (Fig. 5.2). These findings suggest that bighead carp 50 to 120 mm in length exhibit poor anaerobic swimming performance at speeds above 0.5 m s^{-1}. A recent study of swim chamber based fixed velocity performance (Hoover *et al.*, 2012) further supports the data collected; although burst speeds were slightly lower in the current study, the maximum sustained and prolonged swimming speeds were comparable for fish of an equal length.

The capacity of fish to stage successive bursts of locomotion is rarely examined (Castro-Santos, 2004; but see Kemp *et al.*, 2009 for an exception). An inability to negotiate multiple velocity barriers successfully during fish pass ascent could lead to fall back and repeated attempts, thus delaying migration, elevating the energetic cost of passage and increasing fatigue (Quintella *et al.*, 2004). During ascent of the flume, the probability of passage was reduced at each consecutive constriction where high speed swimming was required (Fig. 5.4). Passage failure in this study indicates that the design of technical fish passes should consider cumulative passage efficiency. Therefore, the methodology described here provides a more realistic means of evaluating burst swimming ability to be applied to fish pass design than fixed velocity trials which induce high speed movement from a resting state.

As passage of the constrictions was volitional, behaviour, motivational status, and attractiveness of the conditions encountered, in addition to swimming ability, could have influenced success (Weaver, 1965; Peake and Farrell, 2004; Castro-Santos *et al*., 2013). While unconstrained, fish could exhibit burst-and-coast swimming and exploit low velocity areas available within the flume to conserve energy. Compared to that observed in the swim chamber trials, performance may have been expected to be higher as a consequence (Peake and Farrell, 2004; Hoover *et al.*, 2011). During fixed velocity tests burst speeds of 0.60 - 0.70 m s^{-1} were commonly exceeded by 60 - 100 mm fish. Therefore, passage of the constrictions was predicted to be possible, yet, several individuals failed to ascend under both test conditions (Fig. 5.4). A lack of motivation to ascend flumes can influence volitional passage and may be evident through limited upstream progress against velocities that do not exceed swimming ability (Mallen-Cooper, 1992). However, as fish were generally active in both treatments, exploring the flume throughout the trials and passing the first and second constrictions up to eight and four times, respectively, motivation was unlikely to be the sole determinant of success. Large variation in performance independent of body length was observed during all methods used to assess ability and likely contributed to the inability of some individuals to pass constrictions. The higher passage success under low flow and the positive relationship between success and fish length, a known predictor of swimming ability (Bainbridge, 1958), also supports an influence of swimming ability on ascent. A more holistic understanding of how behaviour as well as physiological capacity can influence fish pass efficiency is required to optimise designs.

Exploitation of low velocity areas was expected within the flume section used for fixed velocity trials (Fig. 5.1), as a performance enhancing strategy. Yet utilisation of flow refugia was common only at low V_{mid} (Fig. 5.3). Other species have been observed swimming close to the channel centre during flume ascent at high speeds, despite occupying edge areas at low bulk velocity (Haro *et al.*, 2004; Castro-Santos, 2005; Castro-Santos *et al.*, 2013). Brook trout (*Salvelinus fontinalis*, Mitchill 1814) and brown trout (*Salmo trutta*, L. 1758) burst swimming upstream remained close to the channel floor but away from the walls, possibly to avoid an unequal pressure distribution across the body, which may cause instability (Castro-Santos *et al.*, 2013). When sustained swimming speeds were exceeded in the current study, fish were more likely to swim erratically in the centre of the channel, avoiding both the walls and floor. The comparable endurance times achieved in the flume and swim chamber may have been due to this behaviour at high bulk velocities. In addition, turbulence can cause instability (Tritico and Cotel, 2010), increase the cost of swimming (Enders *et al*., 2005a), and reduce performance (Lupandin, 2005; Tritico and Cotel, 2010). Higher intensities of turbulence in the open channel may have influenced endurance at all swimming speeds and had the potential to displace fish from low velocity areas.

5.6. Conclusion

Based on the results presented, to allow passage of a high proportion of small bighead carp (50 - 100 mm) upstream, velocities below 0.40 m s^{-1} (lower 90% C.I. of the mean predicted sustained speed for 80 mm fish at 22 °C) are recommended where anaerobic swimming should be avoided (e.g. in fish pass pools, Armstrong *et al*., 2010). This speed was surpassed by the majority of individuals across the temperature range tested (18 – 27 °C). Due to the high variability in endurance at burst and prolonged swimming speeds and low confidence in the subsequent regression models, these are not applied to management recommendations of distance of ascent. If a short burst of high speed swimming is required without the need to maximise distance, then routes with velocities not exceeding 0.60 m s^1 (surpassed by 85% of 50 - 100 mm fish) should be provided. Water velocities may need to be lower (0.50 m s^{-1}) where multiple bursts are required or over a distance of several meters, based on the constriction passage and $U_{\max}$. Provision of regular resting pools may reduce incidences of fall back downstream. Utilisation of low velocity areas available along channel boundaries should not be assumed, as fish may move into the higher velocity mid-channel, depending on bulk flow and turbulence. Of the existing designs, vertical slot or nature like fish passes may be the most suitable options for Asian carp passage, as predicted for other weak swimming benthic fish (Mallen-Cooper, 1992; Bestgen *et al*., 2003; Cheong *et al*., 2006). However, further tests and subsequent monitoring is required due to variable efficiencies in current facilities (Bunt *et al*., 2012).

Invasive bighead carp less than 200 mm long may be blocked if velocities exceed 1.30 m s^{-1} over 50 m (based on maximum swimming speeds reported) at temperatures between 18 and 27 °C. The same criteria should also be appropriate for silver carp which have a slightly weaker swimming performance (Hoover *et al*., 2012). Smooth high velocity culverts may have potential, alongside other devices (e.g. electric barriers and sound and bubble screens; Taylor *et al*., 2005) for impeding movement of Asian carp as part of an integrated management programme. Assuming a linear relationship, a 0.6 m long fish is predicted to be able to swim indefinitely below 1.30 m s^{-1}, and assuming a burst speed equal to approximately 7 *FL* s^{-1}, could pass short distances with velocities below 4 m s^{-1}. However, it cannot be assumed that the relationship between body length and performance at the juvenile life stage will extend to adults as smaller fish often reach higher relative burst speeds (Goolish, 1989; 1991).

This study provides a platform for further iterative research on Asian carp swimming behaviour and performance to guide management practices. Further experimental research employing volitional ascent at a range of high velocities is recommended to evaluate anaerobic performance, swimming speed selection, refuge utilisation, and the influence of turbulence. In addition, validation of performance with wild fish in the field is recommended to ensure fish pass attraction is not compromised by setting conservative water velocities. Further, robust quantification of fish response to potential behavioural deterrents (e.g. hydrodynamic and acoustic cues), in isolation and in combination, is also suggested.

Chapter 6: Influence of hydraulic conditions induced by corrugated boundaries on the swimming performance and behaviour of juvenile common carp (*Cyprinus carpio*).

6.1. Abstract

To facilitate the upstream passage of small fish, corrugated culverts are often preferred over smooth pipes, due to the lower edge and mean cross sectional water velocities created. This benefit could be lost if greater intensities of turbulence induced by wall roughness cause instability and increase the energetic expense of fish locomotion. Common carp (*Cyprinus carpio*, L. 1758) swimming performance and behaviour were evaluated in a flume using four treatments: smooth (control), small (SC), medium (MC), and large (LC) corrugated walls, dependent on corrugation wavelength and amplitude. Individual fish swam at a mid-channel velocity of 0.5 m s^{-1} for 30 min or until fatigue. Swimming performance was quantified by: a) success (completion of 30 min trial) or failure; and b) the time to fatigue (endurance) of those that failed. To evaluate behaviour fish positions were tracked. Occupancy of the area within the MC and LC troughs (concave area where velocity was lowest) was recorded and the influence of fish length tested. For successful fish the effect of treatment on the following dependent variables was assessed: the total distance moved, the mean distance from the flume wall occupied ($Fish_D$), and mean velocity ($Fish_U$) and turbulent kinetic energy (TKE) ($Fish_{TKE}$) experienced. Treatment did not influence frequency of success or endurance. During the MC and LC treatments, troughs were occupied for part of the trial by 50% and 42% of individuals, respectively, independent of fish length. The total distance moved did not differ between treatments. $Fish_D$ was higher for the MC and LC than the control and SC treatments. Despite the availability of lower velocity areas, median $Fish_U$ was higher in the LC treatment (0.51 m s^{-1}) than in any other (median = 0.47 m s^{-1}, 0.44 m s^{-1} and 0.47 m s^{-1} in the MC, SC, and control, respectively). Treatment did not influence $Fish_{TKE}$ which was consistently low (median = 5.3 – 7.7 J m^{-3} per treatment). Fish often appeared to avoid the low velocity locations in the MC and LC treatments in favour of selecting areas with minimal TKE. Under the experimental conditions created, this

study does not support the assumption that corrugated barrels will improve culvert passage.

6.2. Introduction

Culverts can create full or partial barriers to the upstream migration of riverine fish, impeding access to important spawning, rearing, or refuge habitat, and fragmenting populations (e.g. Warren and Pardew, 1998; MacDonald and Davies, 2007; Burford *et al*., 2009; MacPherson *et al*., 2012). Excessive velocities and lack of resting areas in the culvert barrel are a common cause of impediment, especially during high flow (WSDOT, 2012) and for weak swimming species (e.g. burbot, *Lota lota* L. 1758, MacPherson *et al*., 2012; inanga, *Galaxias maculatus* Jenyns 1842, Franklin and Bartels, 2012). As culverts can be tens or hundreds of metres long, fish often need to swim at speeds greater than the oncoming water velocity for several minutes. Designation of suitable water velocities, which are within fish swimming abilities, should be included in the culvert design to improve fish passage (Armstrong *et al.*, 2010; Balkham *et al.*, 2010; Barnard *et al.*, 2013). Although velocity criteria for fish passage are usually based on the bulk cross sectional flow, utilisation of lower velocity zones at the culvert walls may allow small fish to pass upstream even when bulk flow appears to exceed their swimming capability (Ead *et al.*, 2000; House *et al*., 2005).

Compared to smooth walled culverts, corrugated pipes increase the area of low velocity near the wall (Alberta Transportation, 2010). As a result they are often recommended to facilitate the passage of small and weak swimming fish (Clay, 1995; Barnard *et al.*, 2013). However, few studies have quantified the effects of corrugated walls on upstream fish movement through culverts, and when they did the results were mixed (Powers *et al.*, 1997; Johnson *et al.*, 2012). In one study, coho salmon (*Oncorhynchus kisutch*, Walbaum 1792) fry were observed to hold position close to annular and spiral corrugations in an experimental culvert, presumably utilising refuge from the higher mid channel flow (Powers *et al.*, 1997). Yet, passage efficiency of a smooth experimental culvert was greater than for corrugated barrels under several discharge conditions (Powers *et al.*, 1997). In another study, juvenile coho salmon exited a full scale laboratory culvert via a low velocity route created along one channel wall by spiral corrugations (see Richmond *et al*., 2007 for hydraulic analysis of corrugated culverts)

3.5 times more often than along the opposite wall (Johnson *et al.*, 2012). However, there was a negative relationship between passage efficiency and the intensity of turbulence in the reduced velocity zone.

Turbulence can reduce fish stability (Tritico and Cotel, 2010), decrease swimming performance (Lupandin, 2005; Tritico and Cotel, 2010), and elevate the energetic costs of locomotion (Enders *et al.*, 2005a). The hydraulic conditions associated with corrugations, typified by rapid fluctuations in flow (Richmond *et al.*, 2007), may confuse or displace fish into the faster mid channel current, or increase the energetic cost of swimming. Turbulence at the edge may negate any benefit provided by the areas of low velocity created here (Kahler and Quinn, 1998; Boubee *et al.*, 1999; Richmond *et al.*, 2007). Previous attempts to explore the effect of turbulence on upstream fish passage through corrugated culverts have been limited by simplistic fish passage data (e.g. Powers *et al.*, 1997; Johnson *et al.*, 2012) or superficial hydraulic analysis (e.g. Powers *et al.*, 1997).

Corrugation dimensions vary between culvert installations, however, the wavelength and amplitude may influence fish passage success by affecting the intensity and scale of turbulence. The larger the corrugation amplitude the bigger the area of low velocity, yet the greater the intensity of turbulence close to the culvert edge (Behlke *et al.*, 1991; Gerstner, 1998; Bates and Powers, 1998). Furthermore, eddy diameter is influenced by corrugation amplitude and wavelength. In many situations fish swimming ability is negatively related to the intensity of turbulence (Lacey *et al.*, 2011), but if eddy diameter exceeds approximately two thirds of the body length, fish are more likely to be destabilised and their swimming performance reduced (Lupandin, 2005; Webb, 2005; Tritico and Cotel; 2010). Therefore, corrugation dimensions may influence the energetic cost of swimming close to the wall. In addition, the wavelength and amplitude of corrugations determine the size of the area available within the concave troughs and therefore whether individuals are able to occupy this region to gain refuge from high water velocities (Powers et al., 1997; Gerstner, 1998; Gerstner and Webb, 1998; Nikora *et al.*, 2002). Research into this effect has been dominated by substratum ripples rather than wall roughness; for example, Atlantic cod (*Gadus morhua*) gained refuge within substratum ripples only when the wavelength was at least two times greater than their body length, due to an inability to contour their body into a smaller area (Gerstner, 1998).

Previous research on fish passage through corrugated culverts and broader relationships between turbulence, swimming ability and behaviour have tended to focus on anadromous salmonids, notably in North America (Pearson *et al.*, 2006; Lacey *et al.*, 2012; WSDOT, 2012). Although the effects of barriers on the migrations of potamodromous species have gained greater attention in the last two decades (Lucas and Bately, 1996; Lucas and Baras, 2001; Ovidio and Philippart, 2002), restoring habitat connectivity for multispecies continues to represent a considerable challenge (Bunt *et al.*, 2012; Noonan *et al.*, 2012). Furthermore, research on the impact of barriers to movements of potamodromous fish has largely focused on dams and weirs and the design of fish passes (e.g. Lucas and Bately, 1996; Lucas and Frear, 1997; Silva *et al.*, 2012). There has been little attention given to the influence of culverts on this group; however, in areas where there is a high abundance of these structures it is likely they will have some negative impact (Fitch, 1996; Kemp and O'Hanley, 2010; Makrakis *et al.*, 2012).

Upstream dispersal by juveniles to rearing habitat is common for many potamodromous species (Lucas and Baras, 2001; Godinho and Kynard, 2009), and small fish are more likely to be able to utilise localised areas of low velocity (e.g. Powers *et al.*, 1999). Therefore, this study selected a juvenile cyprinid to test the influence of corrugations on the swimming ability and behaviour of a potamodromous species. The common carp (*Cyprinus carpio*, L. 1758) is of considerable economic value in parts of Asia, and is morphologically similar to other cyprinid species of economic value and conservation concern (Zhong and Power, 1996; Lucas *et al.*, 2000). The study aimed to evaluate the influence of corrugated walls on the swimming performance and behaviour of juvenile common carp under four wall roughness treatments: smooth (control), small (SC), medium (MC) and large (LC) corrugations. Swimming endurance was assessed and individual swimming tracks evaluated to explore how treatment influenced swimming behaviour. It was hypothesised that: a) carp swimming performance would be higher in the corrugated treatments than the control due to greater availability of low velocity areas; b) performance would be positively related to corrugation wavelength, due to greater potential to occupy low velocity troughs when wavelength exceeded body length; and c) that fish would hold station in the MC and LC troughs, thus moving little and maintaining position close to the wall in lower velocity areas than in the SC and control treatments.

6.3. Methods

6.3.1. Fish collection and maintenance

Juvenile common carp were obtained from the Hampshire Carp Hatchery, Bishopstoke, UK, and transported (20 min) to the International Centre for Ecohydraulics Research laboratory, University of Southampton, in oxygenated plastic bags on 2 February 2011 (Year 1: $n = 88$, mean ± S.E. total length [TL] = 86.8 ± 0.9 mm, mass = 11.8 ± 0.3 g) and 15 February 2012 (Year 2: $n = 52$, $TL = 85.2 \pm 1.3$ mm, mass = 11.3 ± 0.5 g). A single size range was selected with fish lengths greater than, approximately equal to, and less than corrugation wavelengths for the SC, MC, and LC treatments, respectively. Fish were held in a 900 L aerated and filtered tank under natural photoperiod and ambient temperature in an unheated building (mean water temperature ± S.E. 2011 = 10.3 ± 0.02 °C; 2012 = 10.1 ± 0.02 °C) and fed daily with food sticks. Water quality was maintained through partial exchange (approximately 20% of tank volume) conducted weekly. Trials were completed between 5 and 16 days after fish arrival.

6.3.2. Experimental setup and protocols

Experimental trials were completed in a large, open channel, re-circulatory flume (21.40 m long, 1.37 m wide, 0.60 m deep) powered by three electrically driven centrifugal pumps (maximum discharge = 0.47 $m^3 s^{-1}$). Wire mesh screens (12 mm square) 1.3 m apart created a test section half way along the flume channel. The test section width was reduced to 1.16 m by inserting temporary vertical walls of varying roughness: smooth (control), small (SC), medium (MC) and large (LC) corrugation treatments (Table 6.1).

Fish were placed in perforated containers within the flume for at least 30 min prior to the start of trials to acclimate to water temperature (mean ± S.E. 2011 = 10.2 ± 0.06 °C; 2012 = 11.5 ± 0.08 °C). Individuals were transferred to the test section and swam for 10 min at low velocity (0.2 m s^{-1}) followed by 10 min at an intermediate velocity (0.3 m s^{-1}) to encourage positive rheotaxis. Flow was then increased to the test condition where mid-channel velocity was approximately 0.5 m s^{-1}, dependent on treatment (Fig. 6.1a; discharge and depth remained constant at 0.18 m^3 s^{-1} and 0.26 m, respectively). The test velocity was selected based on the results of preliminary trials which indicated this to be within the prolonged (maintainable for > 20 s but < 200 min) or sustained (maintained indefinitely) swimming speeds of carp (swimming speed categories defined in Beamish, 1978). Trials were ended after 30 min or fatigue (> 3 s impingement on the downstream screen), and total length (*TL*: mm) and mass (grams) of the test fish recorded. A black plastic screen along the flume length prevented visual disturbance by the observer and fish behaviour was recorded using an overhead camera (2 m above flume floor). For analysis it was desirable to have close to equal numbers of successful fish in each treatment, however, due to the variability in frequency of success, the total number of fish tested per treatment was unequal (Table 6.1).

Table 6.1. The dimensions of corrugated walls placed in an open channel flume to create four roughness treatments, and the number of juvenile common carp (*Cyprinus carpio*) tested in each. Walls were inserted into a 1.3 m long test section.

Treatment	**Wavelength (mm)**	**Amplitude (mm)**	***n***
smooth (control)	N/A	N/A	37
small (SC)	40	10	26
medium (MC)	76	20	34
large (LC)	150	50	31

6.3.3. Hydraulic conditions

Water velocity was measured at 60% depth along transects perpendicular to flow using two downward and one sideways facing Acoustic Doppler Velocimeters (ADV; Nortek AS, Oslo, Norway), separated by 120 mm to prevent interference. Velocity was recorded at a frequency of 50 Hz for 60 s, using a 3.1 mm sample depth. Dependent on the hydraulic complexity of treatments, between 12 and 32 transects were completed. The distance between transect sample points increased from 0.02 m close to the walls to 0.20 m in the flume centre. Raw data was filtered to remove erroneous spikes using a velocity correlation approach that accounted for all three dimensions of flow (described in Cea *et al.*, 2007). At each point the mean velocity vector (U) was subsequently calculated as:

$$U = \sqrt{\bar{u}^2 + \bar{v}^2 + \bar{w}^2} \tag{6.1}$$

where $\bar{u}$, $\bar{v}$, and $\bar{w}$ are the mean longitudinal, lateral, and vertical velocity components (m s^{-1}), respectively.

The turbulent kinetic energy (TKE) was selected to quantify the intensity of turbulence within treatments because it is a dimensional number directly comparable to other laboratory and field studies (Lacey *et al.*, 2012). The TKE was calculated at each sample point as:

$$\text{TKE (J m}^{-3}\text{)} = 0.5.\,\rho.\,(\sigma_u^2 + \sigma_v^2 + \sigma_w^2) \tag{6.2}$$

where ρ is the density of water and σ is the standard deviation of velocity. The *U* and *TKE* were plotted in ArcView GIS (v. 9.3, ESRI, Redlands, USA) and interpolated using kriging (cell size = 0.5 cm, search radius = 12 point; Fig. 6.1a and b).

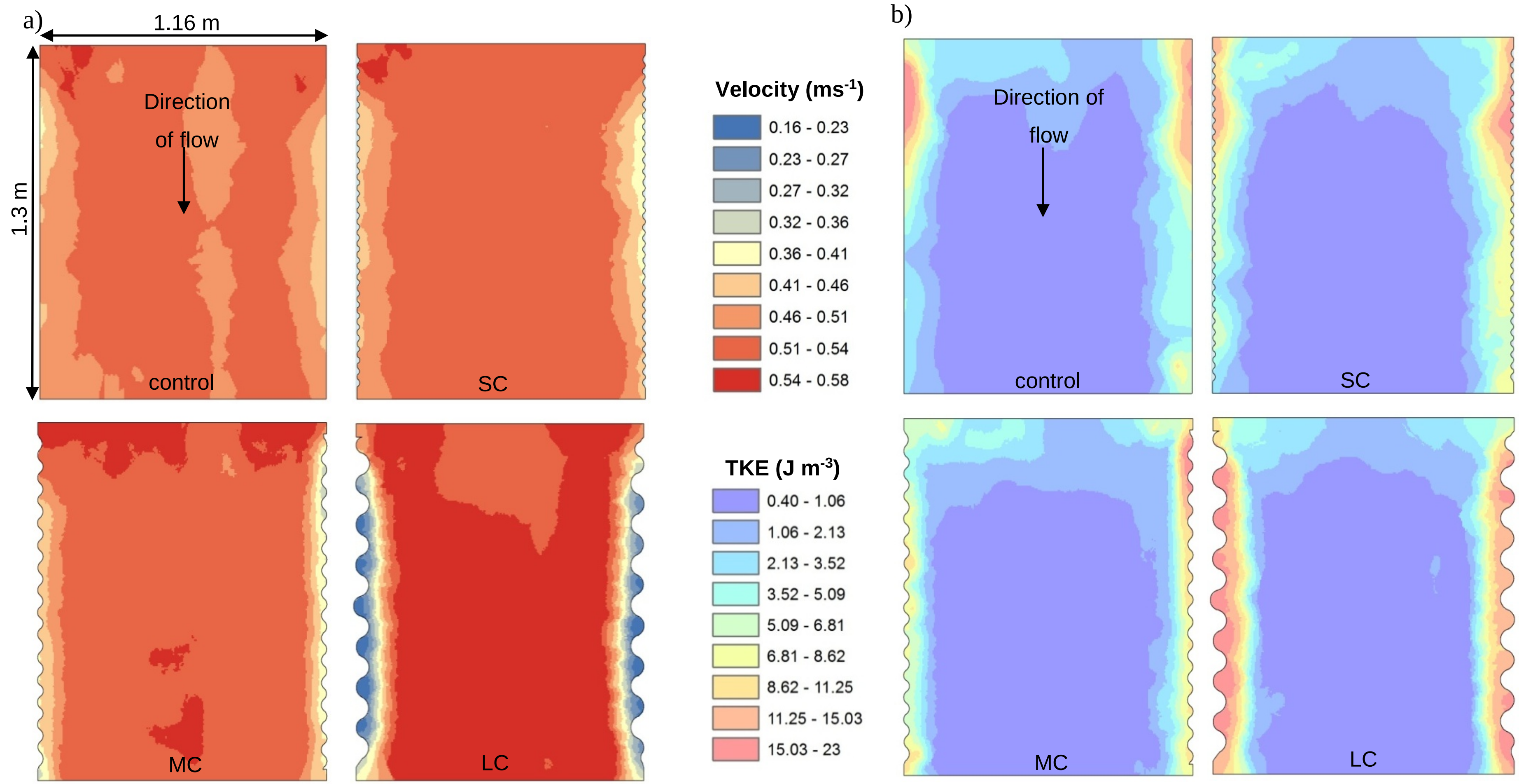


Figure 6.1. a) The mean velocity vector (*U*), and b) Turbulent kinetic energy (TKE) profiles for four treatments used to test the effect of wall corrugations on the swimming performance and behaviour of juvenile common carp: smooth (control), small (SC), medium (MC) and large (LC) corrugation walls. The test section was created in a 21.4 m long flume at the International Centre for Ecohydraulics Research laboratory. Point velocity data were collected using three Acoustic Doppler Velocimeters at 60% depth, plotted in ArcGIS, and interpolated using kriging.

6.3.4. Swimming performance

Swimming performance was quantified as: a) the ability to complete the 30 min fixed velocity trial (categorised as success or failure), and b) the time to fatigue (endurance) for those that failed.

A Pearson's chi-square test was used to test for an association between year and success. As there was no association ($\chi^2 = 0.43$, d.f. = 1, $P = 0.51$) all data were combined for analysis. Water temperature and endurance data were log transformed prior to parametric statistical analysis.

Association between success and treatment was tested using a Pearson's chi-square test. The effects of *TL* and water temperature on success were evaluated using two-way factorial ANOVAs with treatment and success included as independent variables. The influence of treatment on endurance was tested using an ANCOVA, with temperature and *TL* included as covariates.

6.3.5. Fish behaviour

Occupancy of the corrugation troughs during the MC and LC treatments (Table 6.1) was recorded for all fish. The SC treatment troughs were too small (40 mm wavelength) for fish to move into the troughs. Because the endurance of failed fish was low and swimming behaviour was frequently erratic, detailed analysis of fish tracks and the hydraulic conditions experienced were completed only for successful individuals. Their head position was tracked manually every second using Logger Pro (v. 3.8.2, Vernier Software & Technology, Oregon, USA) and plotted in ArcView GIS. Using these co-ordinates, the total distance moved during a trial was calculated. For each head location the distance to the closest flume wall (measured from part of corrugation trough furthest from the flume centre) was calculated (mm) and the *U* and TKE experienced extrapolated from the hydraulic data layer. To summarise fish behaviour and the hydraulic conditions experienced, the mean distance from the wall occupied (Fish_D), and the mean water velocity (Fish_U), and TKE (Fish_TKE) experienced during trials were calculated.

Total length was compared between individuals that occupied the trough area for at least part of a trial and those that did not, using a t-test. Assumptions of normality were violated for $Fish_D$, therefore data were log transformed prior to parametric analysis. One-way ANOVAs and Gabriels post hoc tests for unequal sample sizes were used to investigate the relationships between treatment and the total distance moved and $Fish_D$ for successful fish. Due to failure to meet assumptions of normality and an inability to successfully transform the data, the effect of treatment on the $Fish_U$ and $Fish_{TKE}$ were evaluated using Kruskal-Wallace tests. All statistical analysis was conducted using IBM SPSS Statistics v. 19 (IBM Corp, Armonk, NY, USA).

6.4. Results

6.4.1. Swimming performance

Between 38% (MC treatment; Table 6.1) and 58% (SC treatment) of fish successfully completed the 30 min fixed velocity trial under the four conditions tested (Fig. 6.2). There was no relationship between treatment and success (χ^2 = 2.75, d.f. = 3, P = 0.43). Successful fish had a greater *TL* (mean = 88 mm) than those that were unsuccessful (mean = 85 mm) ($F_{1,119}$ = 5.50, P = 0.02). There was no difference in *TL* between treatments ($F_{3,119}$ = 0.86, P = 0.47), nor an interaction between treatment and success ($F_{3,119}$ = 0.43, P = 0.73). Water temperature did not differ between success ($F_{1, 120}$ = 0.73, P = 0.40) or treatment ($F_{3, 120}$ = 0.65, P = 0.59).

There was no relationship between endurance and treatment ($F_{3,61}$ = 0.71, P = 0.55; Fig. 6.3), *TL* ($F_{1,61}$ = 0.34, P = 0.56) or temperature ($F_{1,61}$ = 2.37, P = 0.13).

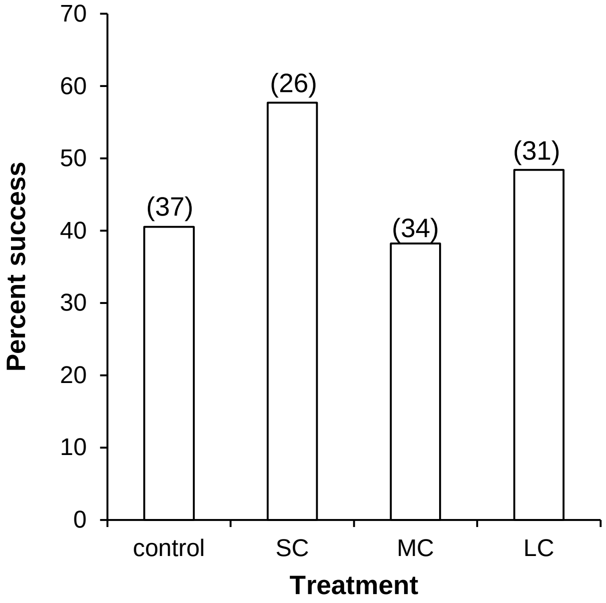


Figure 6.2. The percentage of common carp that successfully swam for the duration of the 30 min fixed velocity trials under four wall roughness treatments: smooth (control), small (SC), medium (MC) and large (LC) corrugations. The total number of fish tested per treatment is shown in parentheses.

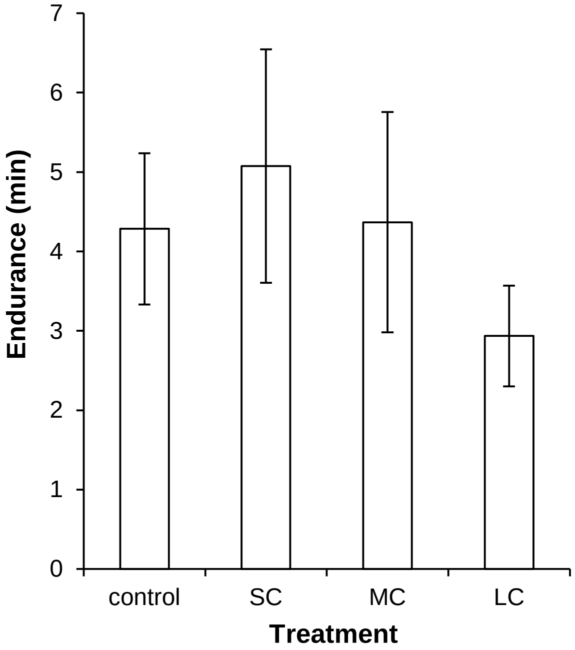


Figure 6.3. The mean endurance of common carp that failed to swim for the duration of the 30 min fixed velocity trials under four wall roughness treatments: smooth (control), small (SC), medium (MC) and large (LC) corrugations. Error bars show ± S.E.

6.4.2. Fish behaviour

Troughs were entered by 50% and 42% of fish in the MC and LC treatments (Table 6.1), respectively (Fig. 6.4). Of those that failed, 43% (MC) and 25% (LC) occupied the troughs for part of the trial, compared with 69% (MC) and 60% (LC) of those that successfully completed the fixed velocity tests. There was no influence of *TL* on trough use (MC: $t_{31} = 0.60$, $P = 0.55$, LC: $t_{29} = -0.76$, $P = 0.45$).

One successful fish in the control and two in each corrugation treatment held position in the centre of the upstream screen for the majority of the 30 min trial (mean distance from wall > 20 cm, S.D. < 10 cm). These fish were excluded from further behavioural analysis. For the remaining fish, there was no difference in the total distance successful individuals swam between treatments ($F_{3,54} = 2.47$, $P = 0.07$). The Fish$_D$ differed between treatments ($F_{3,47} = 3.83$, $P = 0.02$; Fig. 6.5), with that for the LC (mean ± S.E. = 93.2 ± 22.3 mm) being greater than for the SC (33.5 ± 2.8 mm).

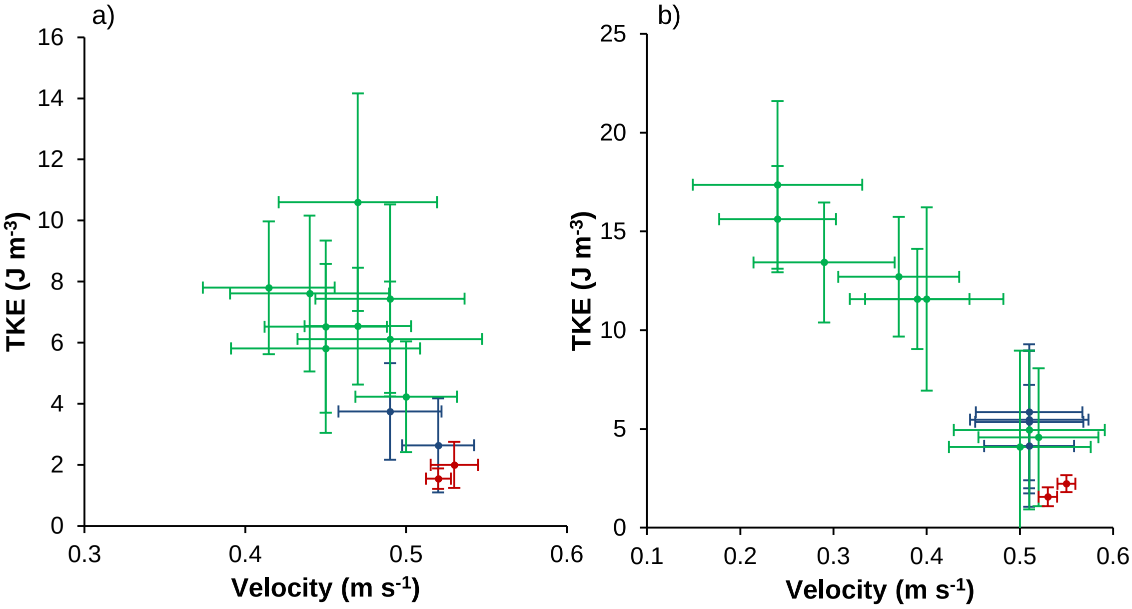


Figure 6.4. The mean (point) and standard deviation (error bars) of velocity and turbulent kinetic energy, experienced by individual common carp that successfully swam for the 30 min duration of a fixed velocity trial under: a) medium, and b) large corrugation treatments. Fish either occupied (green) or did not occupy (blue) corrugation troughs (concave area between peaks) for part of the trial. Red points denote those fish that maintained position in the centre of the upstream screen for the majority of the trial (mean distance from wall > 20 cm; S.D. < 10 cm) and which were excluded from further behavioural analysis.

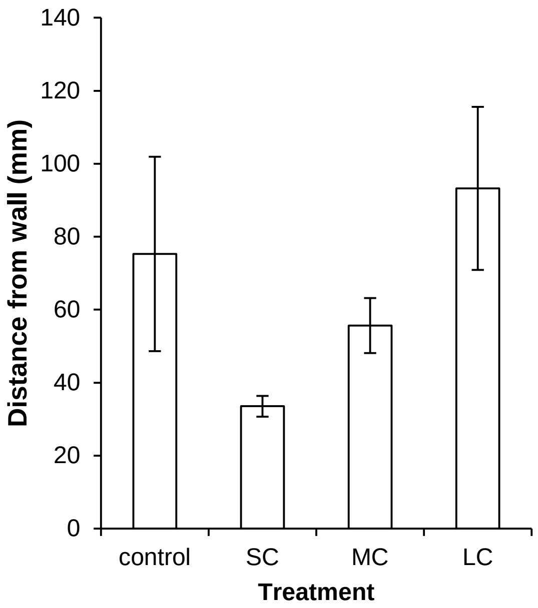


Figure 6.5. The mean and standard error of the mean distance from the flume wall ($Fish_D$) occupied by common carp that successfully swam for the duration of a 30 min fixed velocity trial under four wall roughness treatments: smooth (control), small (SC), medium (MC) and large (LC) corrugations.

The $Fish_U$ for successful individuals was influenced by treatment (Fig 6.6a; Kruskal-Wallis χ^2 = 11.01, P = 0.01), being highest in the LC (median = 0.51 m s^{-1}) and lowest in the SC treatment (0.44 m s^{-1}). In the LC treatment (Table 6.1), $Fish_U$ varied considerably between individuals due to the exhibition of different swimming behaviours (Fig. 6.4). All those experiencing a mean velocity of less than 0.4 m s^{-1} spent time within corrugation troughs, while the remainder predominantly occupied areas further from the wall. The $Fish_{TKE}$ for successful individuals was not influenced by treatment (Fig 6.6b; Kruskal-Wallis χ^2 = 5.52, P = 0.14) and was consistently low, with the treatment median ranging between 5.3 J m^{-3} (control) and 7.7 J m^{-3} (SC).

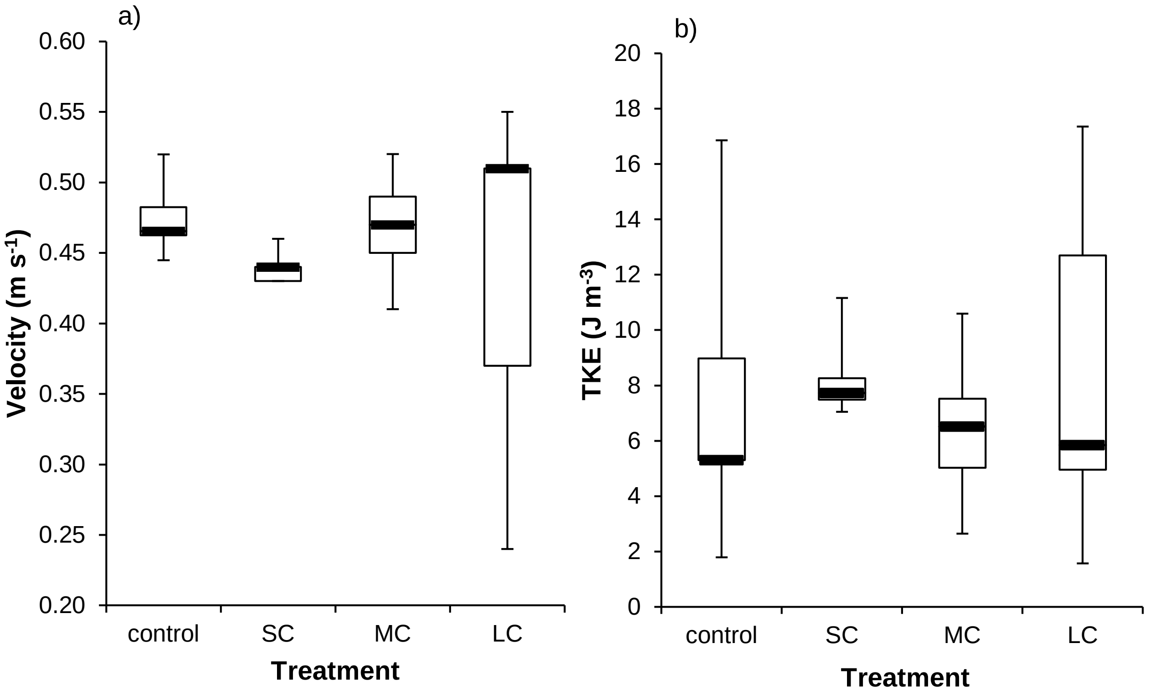


Figure 6.6. The median, interquartile range and minimum/maximum whiskers of the: a) mean trial velocity ($Fish_U$); and b) mean trial TKE ($Fish_{TKE}$) experienced by common carp swimming for 30 min in a fixed velocity trial under four treatments: smooth (control), small (SC), medium (MC) and large (LC) corrugated walls.

6.5. Discussion

Corrugated culverts are often assumed to improve upstream fish passage due to the larger areas of low velocity created at the walls compared to smooth pipes (Ead *et al.*, 2000; Barnard *et al.*, 2013). In this study, the swimming performance of juvenile common carp in an experimental channel was not enhanced under the range of corrugation dimensions tested, when compared to flat walls. On average fish maintained position further from the wall under the medium and large corrugation treatments compared with the small corrugation and control conditions, indicating inconsistent utilisation of the lower velocity areas. This behaviour may have reflected avoidance of higher intensities of turbulence close to the corrugated walls.

Some carp were observed to occupy troughs of both the medium and large corrugations where velocities were between 0.1 and 0.45 m s^{-1}, compared to 0.50 m s^{-1} in mid-channel (Fig. 6.4). Swimming in these lower velocity areas was expected to improve swimming endurance (Bainbridge, 1960; Katopodis and Gervais, 2012). However, neither probability of success (Fig. 6.2), nor endurance of those that failed, was influenced by treatment (Fig. 6.3). In a similar experimental study, Powers *et al.*, (1997) described the utilisation of low velocity areas close to a corrugated culvert wall by coho salmon. Despite the velocity here remaining within their swimming ability, passage success was negatively related to the mean cross-section channel velocity. These observations support the finding from the current study that fish do not necessarily benefit, in terms of enhanced swimming performance, from the occupation of low velocity areas at corrugated culvert walls.

Culvert corrugation amplitude was recommended by Behlke *et al.* (1993) to be at least 5 cm, as smaller ones would insufficiently reduce velocity to benefit fish passage. This principle also applies to riffles on river or sea bed substrates; under experimental flume conditions Atlantic cod only refuged in substratum riffles when their amplitude was at least 2.5 cm, presumably because smaller riffles of the same wavelength did not provide sufficient flow reduction (Gerstner, 1998). However, in this study although the larger amplitude wall corrugations created the lowest flow velocities at the channel edge they also caused the highest intensity of turbulence (Fig. 6.1). As many carp were observed moving away from the wall in the medium and large corrugation treatments (Fig. 6.5), potentially due to the turbulent flow, it is suggested that larger amplitude corrugations are not always the most beneficial for fish passage.

Turbulent flow is energetically costly because fish must constantly stabilise their posture and correct position (Enders *et al.*, 2005a; Tritico and Cotel, 2010). Turbulence can therefore reduce swimming performance (Pavlov *et al.*, 2000; Lupandin, 2005; Tritico and Cotel, 2010) and influence microhabitat selection (Smith *et al.*, 2005; Cotel *et al.*, 2006). A lack of a clear preference for low velocity zones close to the corrugated walls may therefore have reflected a response to the higher levels of turbulence encountered here (Powers *et al.*, 1997; Kahler and Quinn, 1998; Johnson *et al.*, 2012). Although the TKE associated with corrugations in this study was considerably lower than values found in natural riverine environments (Enders *et al.*, 2005b; Tritico and Hotchkiss, 2005), it was comparable with those used in previous experiments of fish swimming performance and energetic costs (e.g. Nikora *et al.*, 2003; Enders *et al.*, 2005a). The total swimming cost for juvenile Atlantic salmon (*Salmo salar*, L. 1758) (mass = 4.3-17.6 g) was on average 25% higher when the TKE was 14.4 compared to 6.9 J m^{-3} ($\bar{u} = 0.23$ m s^{-1}; Enders *et al.*, 2005a). In the large corrugation treatment the TKE close to the wall was between 11 and 23 J m^{-3} (Fig. 6.1), suggesting the cost of swimming in this area may have been elevated due to turbulent flow.

The tendency for many fish to move away from the large and medium corrugation walls (Fig. 6.5) may have reflected a trade-off between the energetic costs of swimming in the turbulent zones close to the corrugated walls and within the higher velocity areas further away. Mean channel velocity will also affect the energetic cost of swimming in areas associated with different intensities of turbulence and could therefore alter the most favourable swimming locations. For example, Atlantic cod only occupied substratum ripple troughs at intermediate velocities (Gerstner, 1998). This behaviour was potentially due to avoidance of turbulent flow at velocities below 0.49 m s^{-1}, because of high instability at low velocities and enhanced energetic expense, and turbulent displacement into the free stream when velocities were greater than 1.09 m s^{-1} (Gerstner, 1998). Further study using different flow conditions is needed to advance our understanding of fish response to wall corrugations.

As the dimension of corrugations are positively related to the size of eddies created (Nikora *et al.*, 2003), this could have also influenced carp behaviour. When eddy diameter is much smaller than fish length, destabilisation is less likely because forces are evenly distributed along the body (Pavlov, 2000; Lupandin, 2005; Tritico and Cotel, 2010). When eddy dimensions exceed a critical threshold, swimming performance is reduced. The eddy threshold for perch (*Perca fluviatilis*, L. 1758) was found to be greater than two thirds of body length, and creek chub (*Semotilus atromaculatus* Mitchill 1818) began to experience body rotation and downstream displacement (spills) when eddy diameter was approximately three quarters of fish length (Tritico and Cotel, 2010). Although eddy size was not quantified in this study, the small corrugated walls would be expected to produce the smallest eddy diameters and to have had a lower impact on fish stability than either of the larger corrugations. Indeed, when compared to the large corrugations, fish in the small corrugation treatment were found closer to the flume walls (Fig. 6.5), and while not statistically significant, the water velocity occupied was lowest (Fig. 6.6a), and the proportion of successful fish (Fig. 6.2) and mean endurance for failures (Fig. 6.3) highest.

In addition to the response to hydrodynamic conditions encountered, position maintenance is influenced by a structure's physical dimensions relative to fish body size. The wavelength and amplitude of corrugations and natural ripples therefore determine whether fish can occupy the troughs (Gerstner, 1998; Gerstner and Webb, 1998; Nikora *et al.*, 2003; Webb, 2006b). Here, some individuals were observed to refuge within the medium and large corrugation troughs, where wavelength was similar to the mean and 1.7 times the mean *TL*, respectively (Table 6.1). The bodies of most fish inhabiting freshwater lotic habitats are more flexible in the lateral than vertical direction (Webb, 1984). This may explain why carp could contour their bodies to allow flow refuging in wall corrugations similar to their body length, whereas Atlantic cod required the distance between substratum ripples to be greater than twice their body length before exhibiting flow refuging behaviour (Gerstner, 1998; Webb, 2006b).

6.6. Conclusion

This study provides a fine scale evaluation of fish swimming behaviour in response to the hydraulic conditions created by corrugated walls. The findings indicate that corrugated barrels may not always improve passage efficiency of culverts for small fish and that the influence of behaviour is an important consideration in assessing and designing less environmentally damaging river infrastructure. Further investigation over a range of flows will be useful as the response to turbulence depends on velocity magnitude (Gerstner, 1998; Smith *et al.*, 2005; Cotel *et al.*, 2006). Evaluation of eddy length scales associated with different corrugation dimensions and the relationship with swimming performance and behaviour could advance optimal culvert design.

Chapter 7: Relationship between European eel (*Anguilla anguilla*) swimming behaviour on encountering accelerating flow and infection with non-native parasites.

7.1. Abstract

The impacts of non-native parasites and river engineering are both suggested to be contributory factors in the decline of the European eel (*Anguilla anguilla,* L. 1758), but their combined effects have not been investigated. The relationship between *Anguillicoloides crassus* (Kuwahara, Niimi and Hagaki 1974)*, Pseudodactylogyrus bini* (Kikuchi 1929) and *P. anguillae* (Yin & Sproston, 1948) infection on the behaviour of downstream migrating silver eels as they encountered accelerating water velocity, common at engineered structures where flow is constricted (e.g. weirs and bypass systems), was evaluated in an experimental flume. The probability of reacting to, and rejecting, the velocity gradient was positively related to *A. crassus* larval, adult, and total abundance. High abundance of *Pseudodactylogyrus* species reduced this effect, but *A. crassus* was the strongest parasitic driver of behaviour and was positively related to delay in downstream passage. Delayed downstream migration at hydraulic gradients associated with riverine anthropogenic structures could result in additional energetic expenditure in migrating eels already challenged by *A. crassus* infection. Future management to aid European eel recovery should therefore account for the combined impact of barriers to migration and eel health on passage, escapement and spawner quality.

7.2. Introduction

Recruitment of the European eel (*Anguilla anguilla,* L. 1758) has declined by more than 90% since the early 1980s (ICES, 2013) and the stock is considered outside safe biological limits (ICES, 1999). A number of factors have been suggested as contributors to explain this decline, including: oceanic conditions (Baltazar-Soares *et al*., 2014); overfishing (Moriarty & Dekker, 1997); pollution (Robinet and Feunteun, 2002); habitat fragmentation (Winter *et al*., 2006); and parasitism and disease (Kirk, 2003; Ginneken *et al*., 2005). Ultimately, there is no consensus over the cause and it appears likely that a combination of factors led to the population crash and continue to prevent recovery (reviewed in: Feunteun, 2002).

Three eel specific parasites, *Pseudodactylogyrus anguillae* (Yin & Sproston, 1948), *P. bini* (Kikuchi 1929), and *Anguillicoloides crassus* (Kuwahara, Niimi and Hagaki 1974), were introduced to Europe through the eel trade in the late 1970s and early 1980s and spread rapidly across the continent (Kirk, 2003; Buchmann, 2012). The European eel is more susceptible to these invasive parasites than the original host, the Japanese eel (*A. japonica*). As a result their intensities can become unusually high (Tarashewski, 2006; Fang *et al*., 2008), and cause greater pathogenic impacts than native parasite species (Kennedy, 2007).

Pseudodactylogyrus anguillae and *P. bini* are gill monogenea specific to eels. At very high intensities their attachment and feeding on epithelia and mucus can cause haemorrhaging, hyperplasia of tissue and fusion of lamellae, reducing gill surface area and impairing respiration (Chan and Wu, 1984; Abdelmonem *et al.*, 2010). In wild European eels their abundance was negatively related to body condition (Gérard *et al*., 2013) and in aquaculture facilities severe cases can cause decreased feeding, lethargy, movement to the water surface and areas of low water velocity, and impingement on outlet screens (Buchmann, 2012). Pathogenic impacts of infection are more common in high density farmed conditions (Kennedy, 2007). Although there is currently little evidence to expect *P. anguillae* and *P. bini* will affect eel migration success, there is the potential for cumulative energetic impacts when *A. crassus* intensity is also high (Køie, 1991).

Juvenile *A. crassus* nematodes migrate from the eels digestive tract to the swimbladder wall, before entering the lumen as adults where they feed on the host’s blood and tissue (Banning and Haenen, 1990). Movement and feeding can lead to inflammation, oedema, fibrosis and haemorrhaging of the swimbladder wall, resulting in a reduced (or in severe cases, collapsed) lumen and altered gas composition (Banning and Haenen, 1990; Molnár *et al*., 1993; Würtz *et al*., 1996). Infection can negatively impact the swimming performance of adult eels (Palstra *et al*., 2007, but see Nimeth *et al*., 2000; Münderle *et al*., 2004 for contradictory results), and this, in combination with organ damage and the energetic costs of sanguivorous activity, is believed likely to reduce the probability of migratory eels reaching their spawning grounds in the Sargasso Sea (Palstra *et al*., 2007; Barry *et al*., 2014). It is also suggested that infected eels may favour shallow coastal areas where possible to ease demand on the compromised swim bladder (Sjöberg *et al*., 2009). However, the relationship between *A. crassus* infection and eel swimming behaviour in freshwater is unknown.

During freshwater eel migrations, barriers, including dams, weirs and sluices, can block access to upstream habitat for colonising juvenile and resident life stages (Moriarty & Dekker, 1997) and impair escapement of silver eels to sea (Calles *et al*., 2010). Hydraulic conditions commonly encountered within these engineered river systems, such as areas of abrupt acceleration of flow (e.g. at weir crests, dam forebays, culvert inlets and the entrance to bypass systems), can delay downstream migration of other fish families, such as salmonids, by inducing behavioural avoidance and retreat upstream (Kemp *et al*., 2008; Enders *et al*., 2009). A number of telemetry studies have reported that eels entering dam forebays often move back upstream several times before selecting a downstream route of passage (reviewed in: Brujis and Durif, 2009). It is unclear whether this behaviour was induced by avoidance of hydraulic conditions, or occurred after contact with physical structures, such as debris screens (Jansen *et al*., 2007). Delays of several days to weeks have been observed (e.g. Pedersen *et al*., 2012; Piper *et al*., 2012), which could increase the energetic cost of migration and predation risk (Rieman *et al*., 1991; Caudill *et al*., 2007), thus reducing the probability of eels reaching their spawning grounds. Additionally, repellent effects at bypass entrances where flow is constricted will enhance the probability of passage through turbines and associated mortality (Castro-Santos and Haro, 2003; Calles *et al*., 2010). Quantifying the extent and causes of behavioural avoidance is important if negative impacts are to be mitigated.

Both parasite infection and delay at barriers to downstream migration have the potential to deplete the energy reserves of European eel embarking on their 5,000 to 6,000 km spawning migration, during which they do not feed. Therefore, a better understanding of eel behavioural response to hydraulic cues at anthropogenic structures, and exploration of the influence of parasites on freshwater migratory behaviour is required. This study aimed to evaluate: 1) the behavioural response of downstream moving silver eels to a velocity gradient representative of those found at bypass entrances; 2) the relationship between *Pseudodactylogyrus* species and *A. crassus* infection and the behaviour exhibited by eels; and 3) the consequent relationship between invasive parasite infection and delay to downstream movement. It was hypothesised that fish energetically compromised by invasive parasites would behave passively to minimise the energetic costs associated with delay.

7.3. Materials and methods

7.3.1. Fish collection and husbandry

Actively migrating silver eels (*n* = 175, mean length ± S.E. = 589 ± 6 mm, mass = 397 ± 14 g) were caught at a permanent eel trap on the River Avon (Hampshire), UK, and transported in oxygenated tanks the following day (6 October 2010) to the International Centre for Ecohydraulics Research laboratory, University of Southampton. Only 6 individuals had an eye index less than the minimum threshold (6.5) used to define the silver life stage (Pankhurst, 1982) (mean ± S.E. = 9.19 ± 0.14), and all except two were over 450 mm long therefore presumed to be female (Durif *et al.*, 2005). All individuals were used in analysis however as they were part of a group of downstream moving adult eels. Fish were held in a 3000 L holding tank, under natural photoperiod and temperature (mean ± S.E. = 13.3 ± 0.06 °C).

7.3.2. Experimental setup and protocol

Experiments were conducted in a re-circulatory flume (21.4 m long, 1.37 m wide, 0.6 m deep), with a maximum flow capacity of 0.47 $m^3 s^{-1}$. A 1 m long velocity gradient (zone B, Fig. 7.1) leading to a constricted channel (4 m long, 0.77 m wide; zone C, Fig. 7.1) was created. Three dimensional water velocities were recorded at 60% depth using an Acoustic Doppler Velocimeter (Nortek AS, Oslo, Norway) sampling at 50 Hz for 60 s, with a sample depth of 3.1 mm. Spurious data were filtered using a maximum / minimum threshold filter (Cea *et al.*, 2007). The mean longitudinal velocity at each point was plotted in ArcGIS (v. 9.3, ESRI) and interpolated using spline methods (Fig. 7.1). The configuration and velocities were representative of those at downstream fish bypass entrances (Gosset *et al.*, 2005; Turnpenny and O'Keeffe, 2005). Assuming a linear gradient, velocity acceleration was 0.45 $m s^{-2}$. Water depth was maintained at 0.24

m. Flume water temperature (mean ± S.E. = 13.9 ± 0.1 °C) was within the upper range of river temperatures during adult silver eel downstream migrations (reviewed in: Brujis and Durif, 2009).

Trials took place during darkness (1900 – 0300 GMT) between 12 October and 3 November 2010. Individual eels were allowed a minimum of one hour to acclimatise to flume conditions prior to release 7 m upstream of zone B and given 30 min to volitionally move downstream. The assignment of fish to trials was based on random capture from the holding tank. Low light cameras were used to record behaviour under infrared illumination (wavelength = 850 nm).

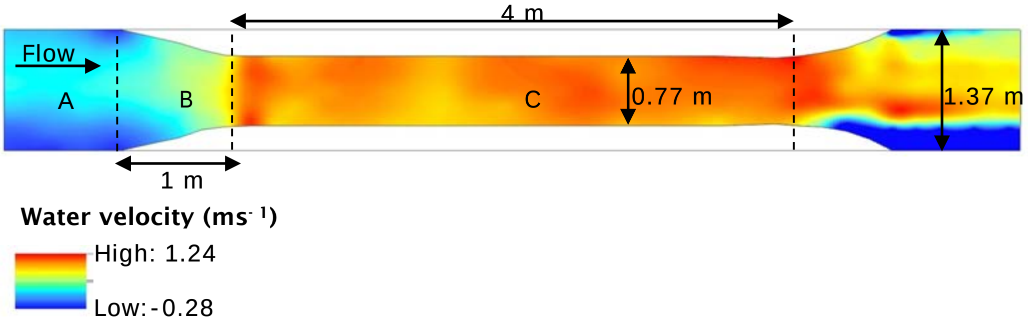


Figure 7.1. Plan of flume configuration at the International Centre for Ecohydraulics Research, University of Southampton. The velocity profile created was used to assess the behavioural response of downstream moving silver eels to accelerating flow caused by a constricted channel. Fish were released 7 m upstream of zone B and behaviour was quantified as they experienced the accelerating velocity in zones B and C. Velocity was measured using an ADV and increased from 0.46 ± 0.03 m s^{-1} to 1.06 ± 0.01 m s^{-1} over the 1 m of zone B.

7.3.3. Post-mortem examination and behavioural analysis

Following behavioural trials eels were transported to Cardiff University or the Environment Agency, Brampton, and killed by an overdose of Benzocaine. A parasite screen of the gills, swim bladder, spleen, gall bladder, heart, musculature and intestinal tract, using low and high-powered microscopy, allowed the overall parasite burden to be assessed for the majority of individuals (see Table 7.1). A reduced screen to evaluate abundance of invasive parasites only was conducted for 27 fish (*n* limited by time availability), and parasite data could not be collected for 11 fish due to loss of the identification tag during transport. Where appropriate, parasites were fixed, cleared or stained to confirm identification (Brown *et al*., 1986; Chubb *et al*., 1987; Moravec, 1994; Gibson *et al*., 2002; Jones *et al*., 2005). Infection parameters followed standard parasite definitions for prevalence (percentage of sampled population infected), abundance (count per fish), and intensity (count in infected fish only) (Bush *et al*., 1997). The abundance of *A. crassus* was split into larval, adult and total found in the swim bladder wall and lumen. Total wet mass was used to calculate the parasite index (*PI* = *A. crassus* mass [mg] / eel body mass [g]). *Pseudodactylogyrus bini* and *P. anguillae* were not differentiated, and their total abundance was determined by doubling the count from the right gill arches, assuming equal distribution across right and left sides (Hockley *et al*., 2011). Species richness and diversity were calculated to summarise the overall parasite community. The Simpson's Diversity Index was calculated as:

$$1\text{-}D, \text{ where } D = \frac{\sum n\,(n-1)}{N(N-1)} \qquad (7.1)$$

n is the total number of organisms of a species, and *N* the total number of organisms of all species. The eye (I_E [Pankhurst, 1982]) and fin index (I_F [Durif *et al*., 2005]) as indicators of silvering, the condition factor (*K* [Fulton, 1904) and fish age were evaluated due to previous evidence of a relationship with *A. crassus* or *Pseudodactylogyrus* abundance (e.g. Fazio *et al*., 2012; Gerard *et al*., 2013), or the potential to impact eel behaviour. Otoliths were aged using the 'burn and crack' technique (Christensen, 1968).

Video records were analysed to quantify eel behaviour. Individuals were categorised into those that approached the constriction (most downstream part of body entered zone B; Fig. 7.1) and those that remained upstream in zone A. Further behavioural analysis was conducted for eels that approached (i.e. entered zone B). Rheotactic orientation at the point of first approach was recorded as negative (facing downstream) or positive (facing upstream). Behaviour in zones B and C was categorised as: a) *passive* (no visible response to the hydraulic gradient and continued downstream movement exiting zone C), b) *reactive* (change in orientation from negative to positive rheotaxis and/or sudden increase in tail beat frequency and burst of upstream movement), or c) *rejection* (*reaction* followed by return to the unconstricted flume, zone A). Individuals that contacted the constriction wall and startled were not included in this analysis (*n* = 21) as it was unclear whether behaviour was a response to the hydraulic conditions or physical contact. Delay was defined as the time between first approach and the point at which the eel fully exited zone C downstream.

7.3.4. Data analysis

All analysis was conducted using IBM SPSS Statistics (v. 20, IBM Corp). To avoid multicollinearity in regression models and to explore possible relationships that could influence eel behaviour, correlations between *A. crassus* infection parameters (larval, adult and total abundance, and *PI*) and *Pseudodactylogyrus* species abundance, and between the invasive parasite infection parameters and eel age, length, mass, K, I_E, and I_F were tested for using Spearman's correlation coefficient (R_s).

Exact Mann-Whitney tests were used to test for differences in *A. crassus* and *Pseudodactylogyrus* infection parameters for fish that did and did not approach the constriction, and between those approaching under positive and negative rheotaxis. The effect of *A. crassus* infection parameters and *Pseudodactylogyrus* species abundance on the probability of eels *reacting* to or *rejecting* the velocity gradient during the first approach were evaluated using binary logistic regression models. Parasite species richness and diversity, water temperature, eel holding time (days spent in holding tanks before trial), age, length, mass, K, I_E , I_F, rheotactic orientation on approach, and two way interactions between all invasive parasite variables were also included as covariates in the initial models to account for possible effects on behaviour. Due to high correlation between eel length, mass and K, I_E and I_F, and *PI* and *A. crassus* abundance, these variables were input into separate starting models and the best predictors identified for final model development. Independent variables and interactions were selected for inclusion in the final model through a backward stepwise likelihood ratio method and examination of the Wald χ^2 statistic, removing variables that did not influence behaviour, to reach the minimum adequate model with the lowest Akaike Information Criterion (AIC) value. Fit was assessed using likelihood ratio tests, Cox and Snell's R^2, and the Hosmer-Lemeshow test. Leverage statistics and residual analysis tested validity of model assumptions. The variables that were found to impact behaviour were analysed for influence on the zone of reaction using Pearson's chi-square (categorical factors) and Mann-Whitney (continuous factors) tests.

Cox regression survival analysis (Cox, 1972; Cox and Oakes, 1984; Castro-Santos and Haro, 2003) was used to assess the impact of invasive parasites on delay. Main effect covariates described for logistic regression were included in the initial model and the minimum AIC was reached through backward likelihood ratio elimination; eel orientation could not be included due to violation of the proportional hazards assumption (Cox, 1972). The Wald χ^2 test was used to assess for a significant effect of covariates on the hazard function, estimated by their coefficients (β). The hazard function was the instantaneous rate of downstream passage for eels that had not yet passed (Castro-Santos and Haro, 2003). A positive coefficient indicated a positive impact on passage rate (i.e. shorter delay). Individuals that did not pass within 30 min were included as censored observations.

7.4. Results

Anguillicoloides crassus prevalence was 81%, mean (± S.E.) intensity was 9.4 (± 0.9), and the maximum was 58 nematodes ($n = 165$). Prevalence of *Pseudodactylogyrus* species was 97%, mean (± S.E.) intensity was 153.1 (± 12.4), with a maximum of 836 ($n = 153$). All fish were infected with either *A. crassus* or *Pseudodactylogyrus* species (Table 7.1). Species richness ranged between 1 and 5 and all native parasites were found at much lower prevalence and intensities (Table 7.1). There was no correlation between *A. crassus* abundance or *PI* and *Pseudodactylogyrus* species abundance, nor between the invasive parasite infection parameters and eel length, mass, K, I_E , I_F , or age (R_s: $P >$ 0.05).

Table 7.1. Summary of the internal parasite screen illustrating the prevalence, mean and range of intensity for each species or genus, the number of eels screened and the mean (± S.E.) of the species richness and Simpsons Diversity Index.

	Species/genus	**Prevalence (%)**	**Mean intensity**	**Intensity range**	**No. fish screened**
Monogenea	*Pseudodactylogyrus* sp.	97	153	1-836	153
Trematoda	*Nicolla gallica* (Dollfus 1941)	9	2	1-3	137
Cestoidea	*Bothriocephalus claviceps* (Goeze, 1782)	8	2	1-3	137
Nematoda	*A. crassus* total (swimbladder)	81	9	1-58	165
	adult (swimbladder)	76	8	1-47	165
	larvae (swimbladder)	50	3	1-34	165
	larvae (gut)	4	1	1-2	138
	Spinitectus inermis (Zeder 1800)	14	8	1-30	138
	Raphidascaris acus (Bloch 1779)	8	1	1-2	138
	Daniconema anguillae (Moravec and Koie 1987)	1	11	2-20	138
	Pseudocapillaria sp.	1	2	2-2	138
	Camallanus lacustris (Zoega 1776)	1	1	1-1	138
	Eustrongylides sp.	1	1	1-1	138
Acanthocephala	*Pomphorhynchus laevis* (Müller 1776)	26	4	1-41	138
	Acanthocephalus lucii (Müller 1776)	9	2	1-3	138
	Acanthocephalus anguillae (Müller 1780)	1	1	1-1	138
Species richness mean (± S.E.) = 2.62 (± 0.09)					129
Simpsons Diversity Index mean (± S.E.) = 0.20 (± 0.02)					129

During the 30 min trials, 9% of fish (16 individuals) failed to approach the constriction. There was no difference in the *PI,* larvae, adult or total *A. crassus,* or *Pseudodactylogyrus* abundance between those fish that did and did not approach (exact Mann-Witney: *P* > 0.05). Eel orientation at first approach was not influenced by any of the invasive parasite infection parameters (exact Mann-Witney: *P* > 0.05).

Discounting those that contacted the structure, 54% of fish approaching the constriction (*n* = 138) moved downstream passively on first approach (Table 7.2). A *reaction* to accelerating velocity on first approach was displayed by 46% of eels approaching the constriction (*n* = 138). *Rejection* of the hydraulic gradient and return upstream to the unconstricted zone A occurred in 78% of all *reactive* eels (36% of total approaching). Following an initial *rejection* of the hydraulic gradient, at least one further *reaction* during subsequent approaches occurred in 53% of these fish.

Table 7.2. The number of fish that exhibited varous behaviours on approach to a flume constriction: a) only fish that approached and did not contact the structure, therefore included in regression models of behavioural response to accelerating flow; b) fish not included in regression models of behavioural response to accelerating flow due to not approaching (i.e. remained upstream in open channel flume) or because of contact with the constriction structure.

Behaviour	*n*	%
a) fish included in behavioural regression models		
Passive	75	54
Total reacted	63	46
Reacted but passed first time	14	10
Reacted and rejected constriction	49	36
Rejected but passed downstream during trial	30	22
Rejected and did not pass downstream within trial	19	14
Total	**138**	
b) Fish not included in behavioural regression models		
No approach	16	43
Excluded due to contacting the constriction	21	57
Total	**37**	
Grand Total	**175**	

Eels that approached under positive rheotaxis were more likely to *react* to the hydraulic gradient than those that approached head first (Wald $\chi^2 = 22.05$, d.f. = 1, $P < 0.001$). The probability of eels *reacting* was also positively related to larval, adult and total *A. crassus* abundance, although only larval abundance was maintained in the final model (Wald $\chi^2 = 11.19$, d.f. = 1, $P < 0.01$) (Table 7.3a, Fig. 7.2). There was an interaction between *A. crassus* larvae and *Pseudodactylogyrus* abundance (Wald $\chi^2 = 7.34$, d.f. = 1, $P < 0.01$); a high *Pseudodactylogyrus* abundance reduced the probability of eels with a high *A. crassus* abundance *reacting*. The probability of *rejection* was increased by positive rheotaxis (Wald $\chi^2 = 33.60$, d.f. = 1, $P < 0.001$, Table 7.3b). The minimum AIC model for rejection also included a positive effect of *A. crassus* larvae abundance (Wald $\chi^2 = 8.09$, d.f. = 1, $P < 0.01$; Fig. 7.2), and an interaction between *A. crassus* larval abundance and *Pseudodactylogyrus* abundance (Wald $\chi^2 = 5.51$, d.f. = 1, $P < 0.05$). There was no effect of parasite richness or diversity, water temperature, eel holding time, age, length, mass, K, I_E, or I_F on the probability of a reaction or rejection.

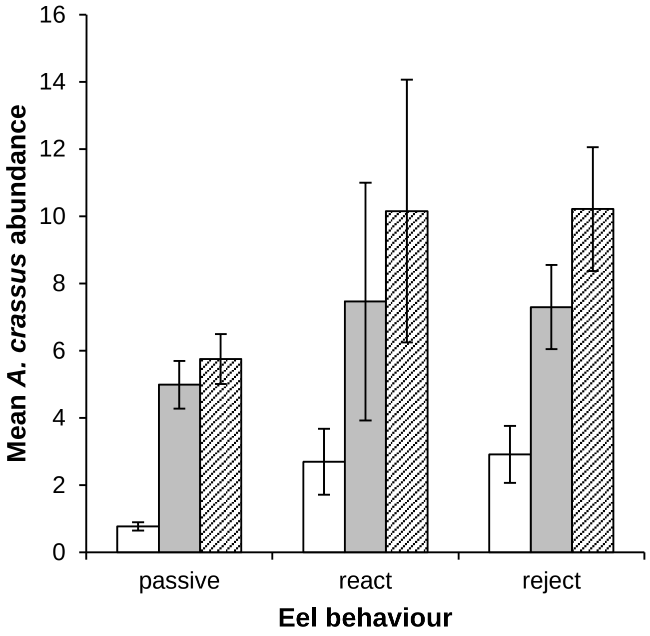


Figure 7.2. The mean abundance of larvae (clear bars), adult (solid bars) and total (hatched bars) *A. crassus* in eels that exhibited *passive* ($n = 69$), *reaction* (change in orientation and/or burst of upstream swimming followed by downstream movement, $n = 13$) or *rejection* (reaction followed by return upstream to the unconstricted flume, $n = 47$) behaviour on encountering accelerating water velocity during the first approach. The error bars represent ± 1 S.E.

Table 7.3. Minimum adequate models for predicting the probability of eels a) *reacting* to the velocity gradient (change in orientation and/or burst of upstream swimming) or b) *rejecting* (reaction followed by return upstream to the unconstricted zone A).

Final model variables	β (S.E.)	Wald χ^2	P	Odds ratio (± 95% CI)
Model a: Reaction				
Orientation during approach	4.10 (0.87)	22.05	< 0.001	60.34 (10.90-334.05)
A. crassus larvae abundance	1.32 (0.40)	11.19	0.001	3.76 (1.73-8.16)
Pseudodactylogyrus sp. abundance	0.001 (0.002)	0.47	0.493	1.001 (0.998-1.005)
A. crassus larvae and *Pseudodactylogyrus* sp. interaction	-0.007 (0.003)	7.34	0.007	0.99 (0.99-1.00)
Model b: Rejection				
Orientation during approach	3.96 (0.68)	33.60	< 0.001	52.42 (13.74-199.91)
A. crassus larvae abundance	0.76 (0.27)	8.09	0.004	2.14 (1.27-3.61)
Pseudodactylogyrus sp. abundance	0.003 (0.002)	1.73	0.188	1.003 (0.999-1.006)
A. crassus larvae and *Pseudodactylogyrus* sp. interaction	-0.005 (0.002)	5.51	0.019	0.995 (0.991-0.999)

Model a: $\chi^2 = 71.08$, d.f. = 4, $P < 0.001$, Cox & Snell $R^2 = 0.45$, Hosmer & Lemeshow $\chi^2 = 8.68$, d.f. = 8, $P = 0.37$.

Model b: $\chi^2 = 65.66$, d.f. = 4, $P < 0.001$, Cox & Snell $R^2 = 0.43$, Hosmer & Lemeshow $\chi^2 = 10.23$, d.f. = 8, $P = 0.25$.

Slightly higher numbers of eels *reacted* in zone B than C (60 and 40%, respectively). Fish that approached under positive rheotaxis were more likely to *react* in zone B ($\chi^2 = 16.72$, d.f. = 1, $P < 0.001$). There was no effect of the invasive parasite parameters on zone of reaction (Mann-Witney: $P > 0.05$).

Of the fish that *rejected* the constricted channel ($n = 49$), 39% did not pass downstream within the 30 min trial, equivalent to 14% of the total eels approaching the constriction (Table 7.2). Delay was positively affected by total and larvae *A. crassus* abundance; in the minimum AIC model a negative coefficient ($\beta = -0.21$, Wald $\chi^2 = 7.17$, d.f. = 1, $P < 0.01$) revealed that high *A. crassus* larval abundance resulted in a slower passage rate (model $\chi^2 = 9.55$, d.f. = 3, $P < 0.05$). Neither *Pseudodactylogyrus* species abundance nor the interaction between *A. crassus* and *Pseudodactylogyrus* abundance impacted delay (*Pseudodactylogyrus* : Wald $\chi^2 = 0.39$, d.f. = 1, $P = 0.53$; interaction: Wald $\chi^2 = 3.18$, d.f. =1, $P = 0.07$).

7.5. Discussion

Contrary to the hypothesis, *Anguillicoloides crassus* abundance was positively related to the probability of downstream moving silver eels avoiding accelerating water velocity and retreating back upstream (Fig. 7.2). While high abundance of *Pseudodactylogyrus* species reduced this effect, *A. crassus* was the strongest parasitic driver of behaviour (Table 7.3) and high abundance resulted in delay to downstream passage. This study demonstrated for the first time a possible energetic cost of *A. crassus* induced through host behavioural change. When combined with a decreased swimming performance (Palstra *et al*., 2007) and impaired swim bladder function (Würtz *et al*., 1996), energetic costs could reduce the probability of European eels successfully completing their spawning migration.

Invasive parasites often have higher virulence and greater pathogenic impacts in a novel host (Britton *et al.*, 2011; Meeus *et al.*, 2011; Lymbery *et al.*, 2014), which can also lead to behavioural changes as a by-product of infection (Taraschewski, 2006; Fang *et al*., 2008). In this study, behavioural differences associated with high intensities of invasive parasites were observed in silver eels (Table 7.3; Fig.7.2). Although prevalence has stabilised and intensities decreased in some areas of Europe since an initial peak following introduction (Kangur *et al.*, 2010; Bernies *et al.*, 2011), intensities of *A. crassus* in European eel remain high (Table 7.1) compared to those in wild and farmed Japanese eel (Münderle *et al.*, 2006; Han *et al.*, 2008). *Pseudodactylogyrus bini* and *P. anguillae* are also found at greater intensities and appear to mature faster in European eel (Fang *et al*., 2008). The Japanese eel has evolved defence mechanisms for

Pseudodactylogyrus species and *A. crassus*, as indicated by frequent observation of dead encapsulated *A. crassus* larvae in both naturally and experimentally infected fish (Knopf & Mahnke, 2004; Münderle *et al*., 2006).

Avoidance of accelerating flow is likely an evolutionary response to natural constrictions or waterfalls, exhibited by fish where there is the potential for injury or disorientation and increased susceptibility to predation (Kroese & Schellart, 1992; Enders *et al*., 2009). Adult eels with an *A. crassus* intensity greater than 10 were observed to have a 19% reduction in maximum swimming speed (Sprengel & Lüchtenberg, 1991). As velocities in the constricted section of flume (Fig. 7.1) approached the maximum threshold of average adult eel burst swimming performance (Clough *et al*., 2004), the greater avoidance of this area by fish hosting a high abundance of *A. crassus* may have reflected efforts to compensate for a lower ability to escape danger. Alternatively, variation in parasite burden may have been a result of intrinsic differences in behaviour between individuals which influenced the probability of infection. For example, a positive relationship between *A. crassus* abundance or swim bladder damage and eel body condition or size relative to age (Lefebvre *et al*., 2012; Gérard *et al. 2013*) may be linked to levels of foraging activity rather than a consequence of infection. More active fish may consume more paratenic hosts and increase the probability of *A. crassus* infection (Lefebvre *et al*., 2013).

Various energy conservation strategies have been observed in parasitised fish with reduced swimming ability (e.g. later flight response to a threat, Binning *et al*., 2014; limited dispersal range, Horký *et al.,* 2014). Gill damage from *Pseudodactylogyrus* in aquaculture conditions can cause reduced activity levels (Buchmann, 2012). The interaction between *Pseudodactylogyrus* and *A. crassus* abundance on eel behaviour supports a more passive, energy saving behaviour in wild eels heavily infected with the former species (Table 7.3). As this was only apparent when *A. crassus* was also high it suggests that only when combined with an additional stressor will *Pseudodactylogyrus* species impact eel behaviour. Further study is required to understand fully the behavioural strategies employed by individuals heavily infected with *A. crassus* in isolation, versus those with high intensities of *Pseudodactylogyrus* species, relative to control uninfected fish. Furthermore, the influence of previous infection and organ damage on behaviour should be considered.

Although a much lower proportion of eels (46%) showed a reaction or rejection to the velocity gradient (Table 7.2) than similar laboratory studies have reported for salmonids (e.g. up to 95% of brown trout (*Salmo trutta*, L. 1758) show a reaction, Vowles & Kemp, 2012), this indicates that eels will respond to hydraulic cues as well as physical structures. Furthermore, a greater avoidance of velocity gradients at dam bypass entrances will reduce passage efficiency for eels parasitised with *A. crassus* and increase delay. Avoidance behaviour should therefore be accounted for in future bypass design, to ensure the hydraulic conditions at the entrance encourage efficient downstream eel passage. To achieve this, further research on eel behaviour at different velocity gradients is required both in controlled laboratory conditions and in situ.

7.6. Conclusion

To complete their spawning migration European eels travel up to 6,000 km, during which they do not feed (Schmidt, 1923; Tesch, 2003), and must maintain sufficient energy reserves for successful reproduction (Thillart *et al.*, 2008). Infection with *A. crassus* elevates the cost of swimming at optimal speeds by approximately 20%, demonstrating an energetic cost which presumably will affect the eel throughout its migration (Palstra *et al*., 2007). Although the impact of *Pseudodactylogyrus* on swimming performance has not been investigated, it is feasible that any impairment to respiration could exacerbate the effects of *A. crassus* to increase demand on energy stores. This study demonstrates a further possible energetic cost due to *A. crassus* infection. Delay as a result of rejecting the constricted flume was relatively short due to the experimental duration and 86% did move downstream in the trial duration. However, there was a limited area within which eels could explore for alternative routes. *In situ*, radio-telemetry studies have shown eels delayed from a few minutes to several weeks at dams where hydraulic gradients are common (Haro *et al*., 2000a; Winter *et al*., 2006; Jansen *et al*., 2007). Eels occasionally retreat upstream several kilometres before returning to the dam (Pedersen *et al.*, 2012) and can approach several times before finally passing downstream (Behrmann-Godel and Eckmann, 2003; Travade *et al.*, 2010). Furthermore, as European rivers are heavily fragmented by anthropogenic structures the cumulative impact of multiple delays could be considerable (Piper *et al*., 2013), although no data are currently available to quantify the impact on energetic costs, lipid reserves, or spawning success. The results of this study suggest that the combined effect of barriers and parasite infection on energetic costs during migration should be recognised in eel conservation efforts to promote passage, escapement and spawner quality.

Chapter 8: Corner and sloped culvert baffles improve the upstream passage of European eels (*Anguilla anguilla*)

8.1. Abstract

Installation of baffles intended to improve fish passage through culverts can reduce discharge capacity and trap debris, increasing flood risk. A sloping upstream face may reduce this risk, but new designs must be tested for fish passage efficiency. The European eel (*Anguilla anguilla*, L. 1758) is a critically endangered species, yet the suitability of even common baffle types to aid upstream movement has not been tested. This study compared the water depth, velocity, turbulent kinetic energy (TKE), and upstream passage performance of yellow-phase eels, between three 6 m long culvert models: smooth and unmodified (control); containing corner baffles (treatment 1); and with prototype sloped baffles installed (treatment 2). Passage of individual fish was assessed during 25 one-hour trials per model. Performance was quantified as entrance efficiency, number of entries per fish, passage efficiency, and overall efficiency. Total and passage delay, and successful passage time were also evaluated. Despite some individuals being able to swim against unexpectedly high water velocities (> 1.5 m s^{-1} for 4 m), passage performance in the control was poor, with an overall efficiency of 28%. Compared to the control, both treatments increased the mean centreline water depth by approximately 0.11 m, created heterogeneous flow conditions with low velocity resting areas, and reduced maximum velocities. As a result, entrance rate and all efficiency parameters were higher for the treatments (overall efficiency = 84%) than for the control, despite longer passage delay. The TKE was slightly higher in treatment 2 than 1, but there was no difference in water depth or overall efficiency. The findings show that both corner and sloped baffles can mitigate for impeded upstream adult eel movement. The extent to which the sloping upstream face will improve debris transport should be explored further.

8.2. Introduction

Culverts installed to convey watercourses under roads, railways and other infrastructure provide a less costly alternative to bridges. The river channel is usually constricted through a box, arch or pipe, with low channel roughness to maximise hydraulic capacity and reduce the probability of sediment and debris accumulation (Clay, 1995). However, rapid water velocities under high flows, insufficient depth at low discharge, and perching of the culvert outlet due to scouring of the downstream river bed, can fully or partially block upstream movement of aquatic organisms, including fish (Larinier, 2002d). As a consequence, access to essential habitat (e.g. for spawning, feeding or rearing: Gibson *et al*., 2005; Sheer and Steel, 2006) is impeded and upstream fish species richness and abundance reduced (Burford *et al*., 2009; Franklin and Bartels, 2012; MacPherson *et al*., 2012).

In recognition of the impact culverts can have on fish passage, design criteria now commonly include recommendations to maintain ecological connectivity (e.g. Balkham *et al*., 2010; Schall *et al*., 2012). Where watercourses support migratory fish, new culverts should meet hydraulic criteria for passage, based on the swimming and leaping ability, and body depth, of the target species (Furniss *et al*., 2006; Caltrans, 2007; Armstrong *et al*., 2010; Barnard *et al*., 2013). At impassable culverts, the installation of retrofits can enable fish passage. When perched, weirs downstream of the outlet increase the tailwater depth, facilitating entry. Placement of bed substrate or baffles within the culvert lowers the water velocity, increases depth, and provides resting areas for fish moving upstream (e.g. Rajaratnam *et al*., 1988; 1989; Ead *et al*., 2002; Balkham *et al*., 2010; Feurich *et al*., 2011). A number of common baffle designs exist for different culvert types (overview in Armstrong *et al*., 2010). The corner baffle is often favoured in pipe culverts where passage of a range of species is required (Armstrong *et al*., 2010; Barnard *et al*., 2013). These are weir type baffles with the crest tilted by 10-20°, leaving one culvert wall unobstructed to facilitate the downstream movement of sediment and debris (Barnard *et al*., 2013; Olsen and Tullis, 2013).

Small diameter culverts in urbanised areas are widespread in Europe and baffle installation can reduce discharge capacity and trap debris, increasing flood risk (Barnard *et al*., 2013; Armstrong *et al*., 2010). A sloped upstream baffle face may reduce this risk by facilitating debris flow, but few studies have examined the suitability of this option for fish passage (for exception see Dupont, 2009) or culvert hydraulics (for exception see Stevenson *et al*., 2008). Brown trout (*Salmo trutta*, L. 1758) were observed moving upstream through alternating sloped baffles, but passage efficiency was not quantified

(Dupont, 2009). Computational fluid dynamic (CFD) modelling predicted higher intensities of turbulence downstream of wedge shaped spoiler baffles than a traditional block shaped design of equal height (Stevenson *et al*., 2008). It was assumed this would negatively influence fish passage but no biological testing was conducted.

Historically, culvert baffle design was driven by the requirements of salmonids, predominantly in North America, where considerable research has evaluated upstream movement of adults and, more recently, juveniles (e.g. Dane, 1978; Powers *et al*., 1997; State Coastal Conservancy, 2004; Pearson *et al*., 2006; Mueller *et al*., 2008; Burford *et al*., 2009; WSDOT, 2012). Worldwide, culvert design for passage of non-salmonid species is gaining attention (e.g. Neotropical fish in Brazil [Makrakis *et al*., 2012] and inanga [*Galaxias maculatus*, 1842] in New Zealand [Franklin and Bartels, 2012]). In Europe, providing and maintaining overall ecological connectivity is a key component of the Water Framework Directive (EC, 2000), but mitigating for the impact of a high density of culverts on multiple species has not been widely considered. For example, a recent attempt to identify barriers to fish movement in England and Wales did not include culverts (Environment Agency, 2010), despite a high abundance of these structures.

The European eel (*Anguilla anguilla*, L. 1758) is considered critically endangered due to a 95-99% decline in recruitment since the 1980s (Freyhof and Kottelat, 2010; ICES, 2013). Barriers to the upstream migration of juvenile eels (elvers) (Moriarty and Dekker, 1997; Feunteun, 2002), and dispersal of resident adults (yellow eels) (Ibbotson *et al*., 2002; Feunteun *et al*., 2003), are likely to have contributed to this decline. In 2007, the European Union adopted Council Regulation number 1100/2007 for establishing recovery measures for the European eel. Member states are required to implement eel management plans, which include the provision of passage routes at structures likely to impede migration. Recently, laboratory (e.g. Russon and Kemp, 2011a) and field-based (e.g. Calles *et al*., 2012; Piper *et al*., 2012) experiments have been conducted to quantify swimming performance and behaviour at dams and weirs to improve eel pass designs. As yet there has been little consideration of the impact of culverts on eel movement, with no published studies quantifying passage efficiency (with or without baffles), and little mitigation guidance provided (e.g. Porcher, 2002; Environment Agency, 2011a). For example, in the UK, maximum culvert water velocity criteria are provided for brown trout, Atlantic salmon (*Salmo salar*, L. 1758), and other non-salmonid fish species grouped together, without consideration of anguilliforms (Armstrong *et al.*, 2010). It is often assumed, but not tested, that species with a weak burst swimming performance, including the European eel, will be able to pass a mean cross sectional velocity designed for faster swimming fish by utilising the lower velocity areas close to the culvert wall (e.g. Scottish Executive, 2000).

The suitability of even common baffle designs for eels remains untested, and minimal data are available on the influence of sloped baffles on culvert hydraulics or fish passage. Therefore, this study compared the hydrodynamic characteristics and passage performance for upstream moving European eel in three full-scale model culvert designs at an equal discharge. The pipes were smooth and unmodified (control) or with either corner baffles (treatment 1) or prototype sloped baffles (treatment 2) installed. The study aimed to: 1) determine whether yellow eels could pass the control culvert; 2) evaluate how corner baffles altered culvert hydraulics and whether this affected eel passage performance compared to the control; and 3) assess the difference between eel passage performance and culvert hydraulics between treatments 1 and 2. It was hypothesised that a) eels would not be able to pass the control culvert due to excessive velocities; b) passage performance would be improved in both treatments compared with the control, due to lower velocities created by the baffles; and c) that treatment 2 would result in higher intensities of turbulence (as in Stevenson *et al.*, 2008) than treatment 1 and therefore a poorer passage performance.

8.3. Methods

8.3.1. Fish collection and maintenance

Yellow phase European eels (*n* = 75, mean ± S.E. total length = 439 ± 11 mm, mass = 161 ± 14 g) were collected from the River Meon, Hampshire, using pulsed DC backpack electrofishing equipment on 11 July and 2 August 2011, and transported in aerated containers to the International Centre for Ecohydraulics Research laboratory, University of Southampton (< 1 h transport time). Fish were held in an aerated and filtered 3000 L tank, filled with de-chlorinated water and kept at ambient temperature in an unheated building (mean ± S.E. = 18.50 ± 0.04 °C). Water changes (approximately

20%) were conducted every week to maintain a high water quality ($NO_3 < 50$ mg L^{-1}, $NO_2 < 1$ mg L^{-1}). Trials took place between 15 July and 10 August 2011, and eels were returned to the River Meon on 5 and 18 August 2011 with no mortality.

8.3.2. Experimental setup and protocols

Experimental trials were performed in a large re-circulatory outdoor flume with a trapezoidal cross section (50 m long, 2.1 m wide at the substrate, 0.5 m deep). Discharge was maintained at 66 L s^{-1} during all trials, using an electrically driven centrifugal pump and adjustable inlet gate and outlet weir. A 1.2 m diameter, 6 m long, smooth, high density polyethylene culvert was cut along the horizontal axis, painted white to facilitate filming, and installed on a 2% slope, 38 m downstream of the flume inlet (Fig. 8.1a). The installation created a lip (0.10 m high) from the flume floor to the culvert base, which was reduced by half using mixed diameter rock substrate. Screens (10 mm square mesh) were fitted 3.8 m downstream and 2.8 m upstream of the culvert to contain fish within the test area.

In treatment 1, five corner baffles (0.15 m high, 0.87 m wide, Fig. 8.1a and b) were constructed of 10 mm plywood and installed approximately 1 culvert diameter apart (1 m spacing), and with a baffle height of approximately 0.15 times culvert diameter (within the recommended range for pipe culverts: Caltrans, 2007; Hotchkiss and Frei, 2007). Baffles extended from the right wall of the culvert, when viewed facing downstream, with a crest angle of 10° from horizontal. For treatment 2, prototype sloped baffles were created by adding a sloping 0.4 m long twin-wall polycarbonate sheet to the upstream face of the corner baffles. The slope spanned between the crest and the culvert floor at an average angle of 20° (Fig. 8.1c).

Eel passage was evaluated in 25 trials, each using a single fish, per culvert design (total = 75 trials). Fish were allowed at least one hour to acclimatise to flume conditions in a perforated container located upstream of the test area (mean ± S.E. temperature = 18.52 ± 0.19 °C). An individual was then released 3 m downstream of the culvert outlet in an area of low velocity. Trials were ended after 60 min or when a fish successfully exited the culvert upstream. Experiments were completed during the night (21:45 - 04:00 BST) and filmed using overhead low light cameras under infrared illumination (wavelength =

850 nm). At the end of each trial the eel was anaesthetised in 2-phenoxyethanol solution (1%) and total length (mm) and mass (grams) recorded.

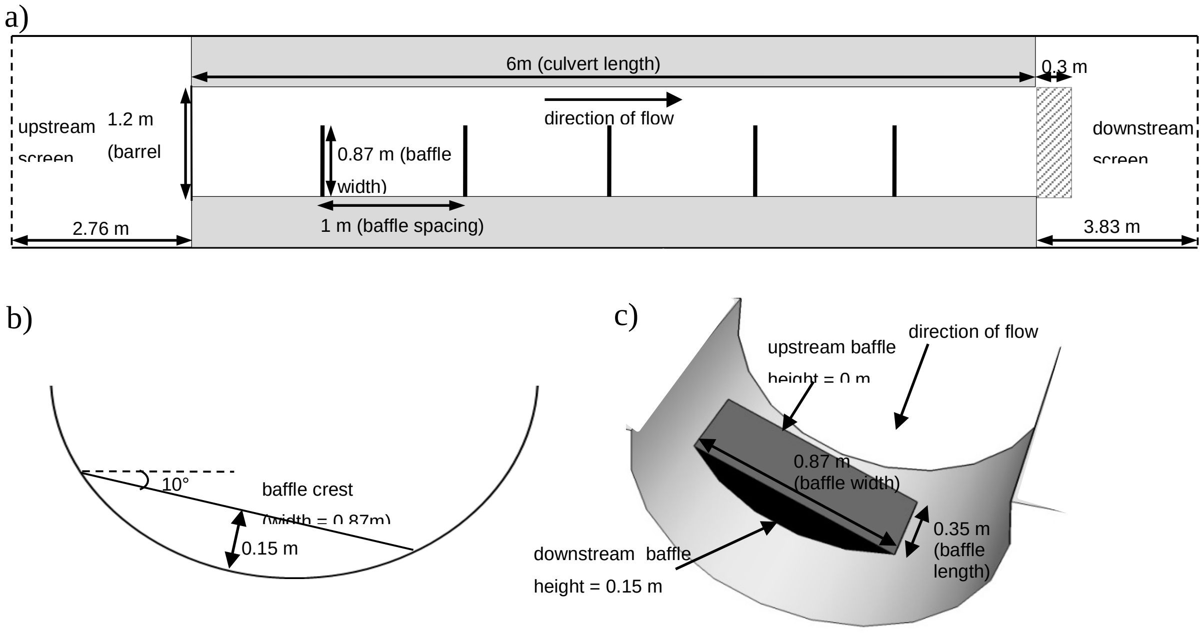


Figure 8.1. Experimental setup of three full scale culvert models: a) Plan view of the model culvert and test area used to evaluate European eel passage performance. The culvert was installed 38 m downstream from the inlet of a large trapezoidal open channel flume (50 m long, 2.1 m wide at substrate, 0.5 m deep). Three designs were assessed: unmodified (control), or with corner baffles (treatment 1, illustrated) or prototype sloped baffles (treatment 2) installed. The hatched area at the outlet represents the approach zone (protruding 0.3 m downstream of culvert outlet).

b) Corner baffle design as viewed looking upstream along the culvert. Baffle width is equal to the 0.87 m crest and baffle length to the 10 mm plywood.

c) Three dimensional diagram of sloped baffle. The slope was created by fitting a flexible 0.4 m long twin-wall polycarbonate sheet to the upstream face of the corner baffles. This spanned between the baffle crest and the culvert floor at an average angle of 20°, creating a 0.35 m baffle length.

8.3.3. Hydraulic conditions

Water depth in each baffle treatment was measured along 41 transects perpendicular to the flow. Due to greater flow homogeneity in the control, measurements were taken at a coarser resolution, at 3 equidistant points along 11 transects (see Fig. 8.2 for sample locations). The mean centreline depth was calculated for each culvert design, not including data collected above the sloping baffle face.

Velocity was measured at 60% of water depth at each sample point. For the two baffle treatments, a downward facing Acoustic Doppler Velocimeter (ADV, Nortek AS, Oslo, Norway) enabled collection of mean (± S.D.) longitudinal (u), lateral (v) and vertical (w) water velocity at each point. Data was collected at 50 Hz for 90 s, with a sample depth of 3.1 mm. Post collection, spurious data were filtered in each flow direction using a maximum/minimum threshold filter. Thresholds were calculated as in Cea *et al*. (2007) as:

$$u_{min} / u_{max} = \bar{u} \pm \sqrt{2 \ln(n)}\, \sigma_u \qquad (8.1)$$

where n is the number of data points, σ the standard deviation of velocity and $\bar{u}$ the mean longitudinal velocity. As water depth in the control was insufficient to allow use of an ADV, mean (10 s) longitudinal water velocity and standard deviation were measured using an electromagnetic flow meter (Model 801, Valeport, Totnes, UK).

In both treatments the turbulent kinetic energy (TKE) was calculated at each sample point as:

$$\text{TKE (J m}^{-3}) = 0.5 \,.\, \rho \,.\, (\sigma_u^2 + \sigma_v^2 + \sigma_w^2) \qquad (8.2)$$

where ρ is the density of water (1000 kg m^{-3}), and the standard deviation of velocity is split into the three directional components. The TKE was chosen as a dimensional number that can be used to directly compare results with other laboratory and field studies (Lacey *et al*., 2011). Fluctuations in flow were highest in the longitudinal and lateral directions. As the TKE could not be calculated for the control, σ_u was used to compare fluctuations about the mean longitudinal velocity between the three culvert designs. The $\bar{u}$ and TKE at each point were plotted in ArcGIS 9.3 (ESRI, Redlands, USA) and interpolated using an inverse distance weighted method (power = 2, search radius = 12 points).

8.3.4. Eel passage performance

An approach to the culvert was defined as movement to within 0.3 m of the outlet. Passage performance was quantified as: 1) entrance efficiency (% of approaching eels that entered the culvert with at least part of their body); 2) number of entries per fish; 3) passage efficiency (% of those eels that entered the culvert that exited upstream); and 4) overall efficiency (% of approaching eels that exited upstream). Delay was split into total and passage delay, measured as the duration (min) between first culvert approach or entry, respectively, and upstream exit. Successful passage time was the duration (s) between final entry into the culvert and exit upstream. Behaviour was recorded as: i) whether individuals ascending the control culvert utilised the lower velocity edge area; ii) the number of low velocity areas between consecutive baffles utilised by each eel during ascent of both treatments; and iii) the percentage of total culvert entries during each treatment (count for all individuals combined) that resulted in retreat downstream to the flume before passing the first baffle upstream of the culvert outlet.

8.3.5. Statistical analysis

To evaluate the effect of baffle type on water depth, the centreline depths at each transect, not including those located on the sloped baffle face, were compared between treatment 1 and 2 using a Wilcoxon signed-rank test.

To assess the effect of eel length and culvert design on the number of times individuals entered the culvert, a negative binomial regression with a log link function was used (McCullagh and Nelder, 1983; Hilbe, 2008). The count was converted to an entry rate to account for variation in time spent downstream of the culvert, by including the natural log of available time (i.e. 60 min or time between release and upstream passage) as an offset variable. Model fit was assessed using the likelihood ratio chi-square test and by examining deviance residuals. Significance of regression coefficients were assessed by the Wald chi-square test.

Binary logistic regression was used to test for effects of eel length and culvert design on the passage and overall efficiencies, by evaluating the probability of passage success. Significance of the covariates was assessed using the Wald chi-square test. Leverage statistics and residual analysis were used to check validity of model assumptions (Zuur *et al.*, 2010), and the model chi-square test, Nagelkerke R^2, and the Hosmer and Lemeshow test to examine model fit.

The influence of culvert design on total and passage delay and successful passage time were analysed using Kruskall Wallace and post-hoc Bonferroni corrected exact Mann-Whitney tests. All analysis was completed using IBM SPSS Statistics version 19 (IBM Corp, Armonk, USA).

8.4. Results

8.4.1. Hydraulic conditions

The mean centreline water depth was 8.55 cm in the control, compared to 19.62 and 19.89 in treatment 1 and 2, respectively. There was no difference between the centreline water depth in treatment 1 and 2 (Wilcoxon $z = -1.13$, $P = 0.26$).

The centreline mean longitudinal water velocity in the control increased from 0.71 m s^{-1} at the culvert inlet to a maximum of 1.69 m s^{-1} at the outlet (Fig. 8.2). The mean transect velocities for mid culvert and the outlet were 1.54 and 1.56 m s^{-1}, respectively. In the treatments, high velocity areas were located immediately downstream of each baffle on the culvert left hand side. The maximum velocities recorded in treatment 1 and 2 were 1.31 and 1.42 m s^{-1}, respectively (Table 8.1). Treatment 2 had greater reverse flows in the low velocity areas between baffles on the right hand side of the culvert than treatment 1 (Fig. 8.2).

The mean standard deviation of longitudinal velocity in the control was 0.03 m s^{-1}, compared to 0.29 and 0.30 m s^{-1} in treatment 1 and 2, respectively. Areas of TKE greater than 200 J m^{-3} were common in both treatments, with peaks of over 600 J m^{-3}. Areas of higher TKE were present on the left hand side of the culvert in treatment 2 than 1 (Table 8.1, Fig. 8.3).

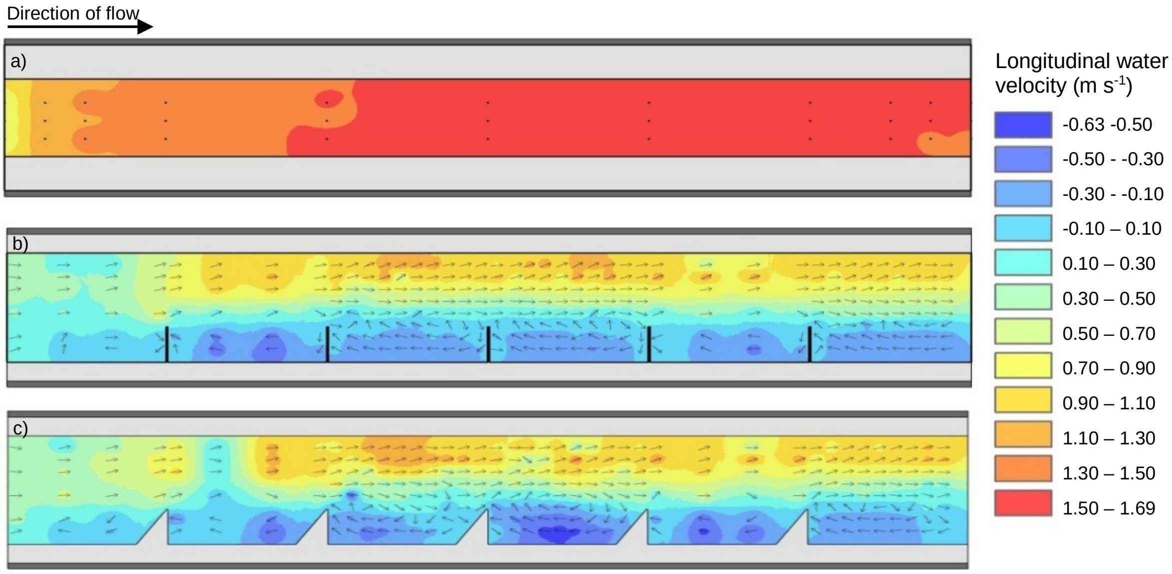


Figure 8.2. Plan view of the 60% depth mean longitudinal water velocity in a 6 m long, model culvert, for three designs: a) unmodified and smooth (control); b) corner baffles (treatment 1); and c) sloped baffles (treatment 2). Longitudinal velocity was collected at the points shown in the control with an electromagnetic flow meter, and at each arrow location in treatment 1 and 2 using an Acoustic Doppler Velocimeter. Arrows show the direction of flow, calculated from the longitudinal and lateral velocity components. Velocity was interpolated between points in ArcGIS.

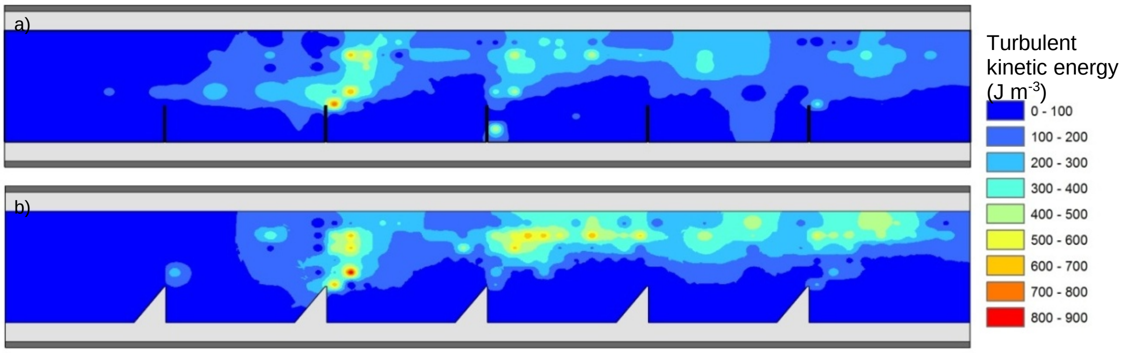


Figure 8.3. Plan view of 60% depth turbulent kinetic energy in a model, 6 m long, culvert with a) corner baffles (treatment 1), and b) sloped baffles (treatment 2) installed at 1 m intervals.

Table 8.1. The mean (with range in parenthesis) of the mean longitudinal water velocity ($\bar{u}$), standard deviation of longitudinal water velocity (σ_u), and turbulent kinetic energy (TKE) at each sample point in a 6 m long model culvert for three designs: unmodified and smooth (control), corner baffles (treatment 1), and sloped baffles (treatment 2). Data was collected at 33 points using an electromagnetic flow meter in the control and at 300 and 313 points using an Acoustic Doppler Velocimeter in treatments 1 and 2, respectively.

Culvert design	**Velocity ($\bar{u}$: m s^{-1})**	**S.D. velocity (σ_u: m s^{-1})**	**TKE (J m^{-3})**
Control	1.43 (0.71 - 1.69)	0.03 (0.00 – 0.0)	na
Treatment 1	0.40 (-0.36 - 1.31)	0.29 (0.03 - 0.79)	128.16 (2.25 - 546.74)
Treatment 2	0.40 (-0.63 - 1.42)	0.30 (0.04 - 0.89)	149.02 (2.15 - 870.22)

8.4.2. Eel passage performance

All fish approached the culvert and were included in passage analysis (Fig. 8.4). Entrance efficiency was 40, 92 and 100% for the control, and treatment 1 and 2, respectively. Entrance rate was affected by culvert design and was on average 9 and 13 times higher for treatment 1 and 2 than the control, respectively (Wald χ^2 = 21.17 and 34.35 respectively, d.f. = 1, $P < 0.001$, Table 8.2). Entrance rate was not significantly different between treatment 1 and 2 (Wald χ^2 = 0.94, d.f. = 1, P = 0.33), and was not affected by eel length (Wald χ^2 = 3.35, d.f. = 1, P = 0.07).

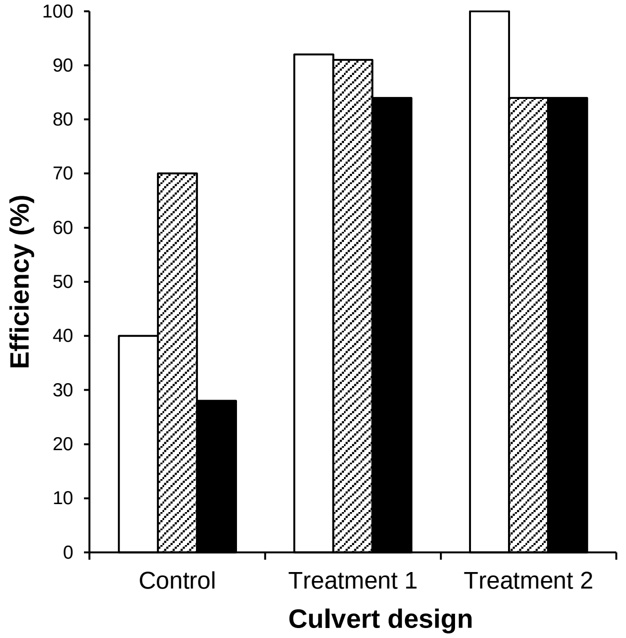


Figure 8.4. Summary of upstream European eel passage performance in three model culvert designs. Clear, hatched and solid bars, respectively, represent entrance (% of approaching eels that entered the culvert), passage (% of eels that entered and then exited upstream), and overall (% of all approaching eels that exited upstream) efficiency.

Table 8.2. Results of a negative binomial regression model with a log link, where number of entrances to the culvert was the dependent variable, and culvert design (reference = control, 1 = corner baffles, 2 = sloped baffles) and eel length were the predictors. The regression coefficients (*β*) and associated S.E., Wald Chi-Square *P* value, and odds ratio with 95% confidence intervals are reported.

			95% C.I. for odds ratio		
Variable	***β*** **(S.E.)**	***P***	**Lower**	**Odds ratio**	**Upper**
Intercept	-9.65 (0.95)	<0.001	0.00	0.00	0.01
Culvert design = 1	2.18 (0.47)	<0.001	3.50	8.86	22.45
Culvert design = 2	2.59 (0.44)	<0.001	5.61	13.34	31.73
Length	0.004 (0.002)	0.07	1.00	1.004	1.008

Model likelihood ratio $\chi^2 = 38.40$, d.f. = 3, $P < 0.001$.

Passage efficiency was 70, 91 and 84% for the control, treatment 1, and treatment 2, respectively (Fig. 8.4). There was no significant influence of culvert design or eel length on passage efficiency (model χ^2 = 7.26, d.f. = 3, P = 0.06). The overall efficiency was 28% for the control, and 84% for both baffle treatments (Fig. 8.4). Overall efficiency was affected by eel length, with larger eels more likely to pass upstream (Wald χ^2 = 7.02, d.f. = 1, $P < 0.01$), and differed between culvert designs (Wald χ^2 = 16.59 d.f. = 2, $P < 0.001$, Table 8.3). Overall efficiency was higher in both treatments than the control, but did not differ between treatment 1 and 2 (Wald χ^2 = 0.05, d.f. = 2, P = 0.82).

Total delay did not differ between culvert designs (Kruskall Wallis χ^2 = 1.86, d.f. = 2, P = 0.40). Passage delay varied between designs (Kruskall Wallis χ^2 = 7.11, d.f. = 2, $P < 0.05$, Fig. 8.5), being longer in treatment 2 than the control (median = 3.17 versus 0.23 min; Mann-Whitney U = 28, $P < 0.05$). After Bonferroni corrections there was no significant difference between the control and treatment 1 (median = 0.65 min; Mann-Whitney U = 33.5, P = 0.03), or between the two baffle treatments (Mann-Whitney U = 174, P = 0.25).

Table 8.3. Results of a binary logistic regression model to assess the impact of culvert design and eel total length on overall efficiency of yellow eel passage through an experimental culvert. The binary dependent variable was passage success and the influence of culvert design was analysed using a simple contrast (reference = control, 1 = corner baffles, 2 = sloped baffles). The regression coefficients (β) and associated S.E., Wald Chi-Square P value and odds ratio with 95% confidence interval are reported.

			95% C.I. for odds ratio		
Variable	**β (S.E.)**	***P***	**Lower**	**Odds ratio**	**Upper**
Constant	-8.28 (2.87)	0.004		0.00	
Culvert design		< 0.001			
Treatment 1	3.11 (0.92)	0.001	3.70	22.53	137.31
Treatment 2	3.30 (0.88)	< 0.001	4.90	27.21	151.29
Length	0.02 (0.01)	0.009	1.00	1.02	1.03

Model χ^2 = 32.38, d.f. = 3, $P < 0.001$, Nagelkerke R^2 = 0.50, Hosmer and Lemeshow χ^2 = 1.18, d.f. = 8, P = 0.99.

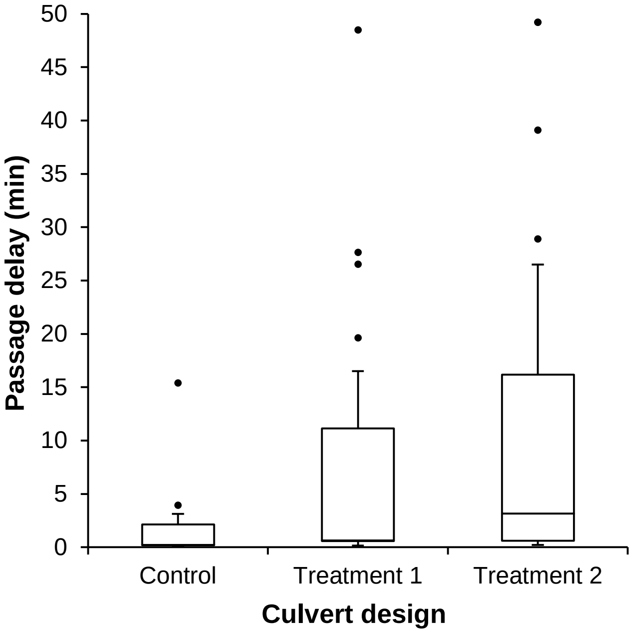


Figure 8.5. Passage delay (time between first culvert entrance and upstream passage) for three model culvert designs: smooth and unmodified (control), corner baffles (treatment 1) and sloped baffles (treatment 2). Data are shown as the median, interquartile range, whiskers at 1.5 x interquartile range or minimum, and outliers. The maximum trial duration was 60 min.

Successful passage time differed between the culvert designs (Kruskall Wallis χ^2 = 17.06, d.f. = 2, $P < 0.01$), being shorter for the control than treatment 1 (median = 14 versus 35 s, Mann-Whitney $U = 5.5$, $P < 0.01$) and 2 (median = 41 s; Mann-Whitney $U = 3.0$, $P < 0.01$). There was no difference between treatment 1 and 2 (Mann-Whitney $U = 167.5$, $P = 0.18$).

Only one eel swam the entire length along the control culvert wall where velocities were lowest. In both treatments, eels commonly moved away from the culvert left hand side to rest in the low velocity areas between consecutive baffles. All 5 of these areas were utilised by 52% of fish in both treatments, which tended to result in a longer successful passage time (Table 8.4). A total of 52 and 100 entries were made by the 25 fish in treatments 1 and 2, respectively. Of these, 54% (treatment 1) and 70% (treatment 2) resulted in retreat downstream to the flume before passage of the first baffle.

Table 8.4. The number of low velocity areas between consecutive baffles utilised by individual yellow eels during upstream ascent of a culvert fitted with corner (treatment 1) and sloped (treatment 2) baffles, and the mean time (with range in parenthesis) taken to pass the culvert (i.e. successful passage time).

	Treatment 1		**Treatment 2**	
Number of low velocity areas utilised	**Frequency of fish**	**Successful passage time (s)**	**Frequency of fish**	**Successful passage time (s)**
1	1	10 (na)	0	na
2	1	18 (na)	3	23 (14-34)
3	6	35 (28-49)	4	33 (24-45)
4	2	29 (26-32)	3	68 (57-84)
5	11	40 (21-54)	11	68 (29-326)

8.5. Discussion

Culverts have the potential to severely impede fish migration due to the creation of adverse hydraulic conditions (Warren and Pardew, 1998). In this study, the low overall efficiency of an unmodified culvert to pass yellow phase European eel upstream caused the structure to form a partial barrier to fish movement. Both corner and prototype sloped baffles were successful in improving entrance and overall efficiency compared to the unmodified culvert (Fig. 8.4). Corner baffles are often recommended for other fish species (Armstrong *et al*., 2010; Barnard *et al.*, 2013) and, therefore, may provide a valuable multi-species mitigation option at culverts that can be difficult to pass. At the discharge tested, although the hydrodynamic conditions were slightly different with the sloped baffles installed compared with the corner baffles, this did not influence eel passage performance. Water depth was also equal with corner and sloped baffles and the angled face may have the potential to improve transport of debris and thus reduce flood risk.

As eels have a relatively low burst swimming ability compared to many other fish species (McCleave, 1980; Environment Agency, 2011a; Russon and Kemp, 2011a), velocity barriers may disproportionally impede their movements. Velocities within the unmodified culvert (Fig. 8.2) were below the Environment Agency maximum culvert criteria for adult brown trout, but at the maximum limit of eel swimming ability for the size range tested (reviewed in: Environment Agency, 2011a). Thus, this likely contributed to the control culvert's low overall efficiency (28%). Furthermore, at these high velocities time to fatigue would be short and passage through a much longer unmodified culvert with similar velocities would likely be impossible (Bainbridge, 1960; Katopodis and Gervais, 2012). The installation of corner and sloped baffles reduced the water velocity throughout the barrel and created lower velocity pools where fish could rest (Fig. 8.2), which was likely a significant factor contributing to the higher passage efficiencies in both treatments. The high velocities, low water depth, and outlet lip may have also contributed to the low entrance efficiency for the control culvert. Although the outlet lip remained during both treatments, the two baffle designs successfully altered the hydrodynamic conditions to enhance entrance efficiency (92 and 100% for corner and sloped baffles, respectively; Fig. 8.4).

Open channel flume studies can result in higher fish swimming speeds than achieved in swim chamber tests where the confined conditions prevent fish from exhibiting natural performance enhancing behaviours to maximise swimming speeds (Peake and Farrell, 2004; 2006; Tudorache *et al*., 2007). A model developed based on the results of swim chamber tests predicted a burst swimming ability of 1.18 to 1.27 m s^{-1} (90% confidence intervals: 0.97 to 1.48 m s^{-1}) for European eels within the range of body lengths (366 - 546 mm) and water temperatures (16.1 – 19.0 °C) used in the unmodified culvert trials (SWIMIT V 3.3. © Environment Agency, 2005, see Clough *et al*., 2004). Yet, a recent volitional study found that silver eels (mean length = 660 mm) at an average temperature of 15 °C could actually traverse velocities of 1.75 to 2.12 m s^{-1} over a distance of about 1 m (Russon and Kemp, 2011a). Swimming performance is lower for yellow than silver eels (Quintella *et al*., 2010), but in this study some fish as small as 366 mm successfully negotiated velocities exceeding 1.5 m s^{-1} along 4 m of the unmodified culvert, before reaching slower flows near the inlet (Fig. 8.2).

The installation of baffles created higher levels of turbulence compared to the unmodified control (Fig. 8.3). Enhanced turbulence is an inherent effect of using structures to reduce water velocity, and alternative designs also produce high intensities of turbulence immediately downstream of baffles (e.g. Morrison *et al*., 2009). Turbulent flow can reduce fish stability and swimming performance (Tritico and Cotel, 2010), and elevate energy expenditure (Enders *et al*., 2005a). Fish with an elongated body morphology, such as eels and lamprey, are perhaps most likely to be destabilised (Liao, 2007), although this has not been quantified. Conversely, it has been suggested that they may, under certain conditions, be attracted to turbulent areas (Russon *et al*., 2010; Piper *et al*., 2012) and utilise reverse flows to minimise energy expenditure (Kemp *et al*., 2011). Although the TKE in both culvert treatments (200-400 J m^{-3}, with peaks of over 600 J m^{-3}) was considerably higher than levels demonstrated to increase juvenile Atlantic salmon swimming costs (Enders *et al*., 2005a; 41.6 J m^{-3}), overall efficiency of eel passage was high. The high passage success suggests that any negative consequences for eel swimming performance were limited, and the improvement in passage performance compared to the control supports the use of baffles over the culvert length tested (Fig. 8.4).

Baffle spacing and dimensions influence culvert hydraulics and determine flow capacity and fish passage success (Rajaratnam *et al*., 1988; 1989; 1990; Caltrans, 2007). The sloped baffle design created slightly higher TKE on the left hand side of the culvert than in the corner baffle model (Fig. 8.3). This finding is analogous to the CFD modelled increase in turbulent flow downstream of wedge shaped spoiler baffles compared to oblong ones (Stevenson *et al*., 2008). Despite hydrodynamic differences between treatments, overall efficiency was equal, and entrance and passage efficiency were similar (Fig. 8.4). However, the time from first culvert entry to exit upstream (passage delay) was greatest for the sloped baffle design (Fig. 8.5). The passage delay within baffle treatments was likely in part due to a longer successful passage time due to resting between baffles during ascent (Table 8.4), an advantage that would enable passage of long culverts whilst minimising energetic expenditure. However, as passage delay differed between treatments and could be up to 50 minutes, other factors also likely contributed and further evaluation under alternative flows are recommended to improve understanding of the influence of hydraulics on passage performance.

Hydrodynamic, physical, and other environmental factors can cause delay and reduce passage at anthropogenic structures by influencing behaviour (Rice *et al*., 2010, Kemp *et al*., 2011). The majority of culvert entries during both treatments resulted in downstream retreat before passage of the first baffle, and this repeated retreat downstream likely contributed to the greater passage delay in treatments than experienced in the control culvert. The high number of entries not resulting in upstream passage auccess was unlikely to be due to poor motivation or swimming ability, as approach efficiency was 100% and overall efficiency high for both treatments. It may have been an outcome of eels' natural tendency to seek cover (Edel, 1975; Tesch, 2003), resulting in exploration of the open channel flume and resting downstream of the first baffle encountered. It is also possible that the substrate oriented, thigmotactic, swimming behaviour described for eels (Russon *et al*., 2010; Russon and Kemp, 2011a) may have discouraged passage when entry occurred on the side of the culvert where baffles were situated. In a similar experimental culvert study, substrate oriented inanga spent long periods of time swimming between full weir baffles without making upstream progress (Feurich *et al*., 2012). Thigmotactic behaviour was blamed for delay of downstream migrating European eels at an experimental overshot weir (0.20 m high) compared to an undershot weir, and the lower passage efficiency for the former (Russon and Kemp, 2011a). Therefore, until further research into behaviour during passage of various designs has been conducted, including in situ field evaluation, baffles which cross the full culvert cross section are not recommended, due to the potential for further delay whilst searching for upstream routes.

The relative change in water depth compared to the control was equal for both baffle designs, indicating that the addition of a sloping upstream face onto the corner baffles did not reduce culvert flow capacity under the conditions tested. This design has the potential to reduce flood risk through reducing the likelihood of debris blockage, without decreasing discharge capacity beyond that caused by standard corner baffles, or reducing eel passage performance. Further laboratory trials followed by evaluation in situ are required to confirm the flood risk benefits.

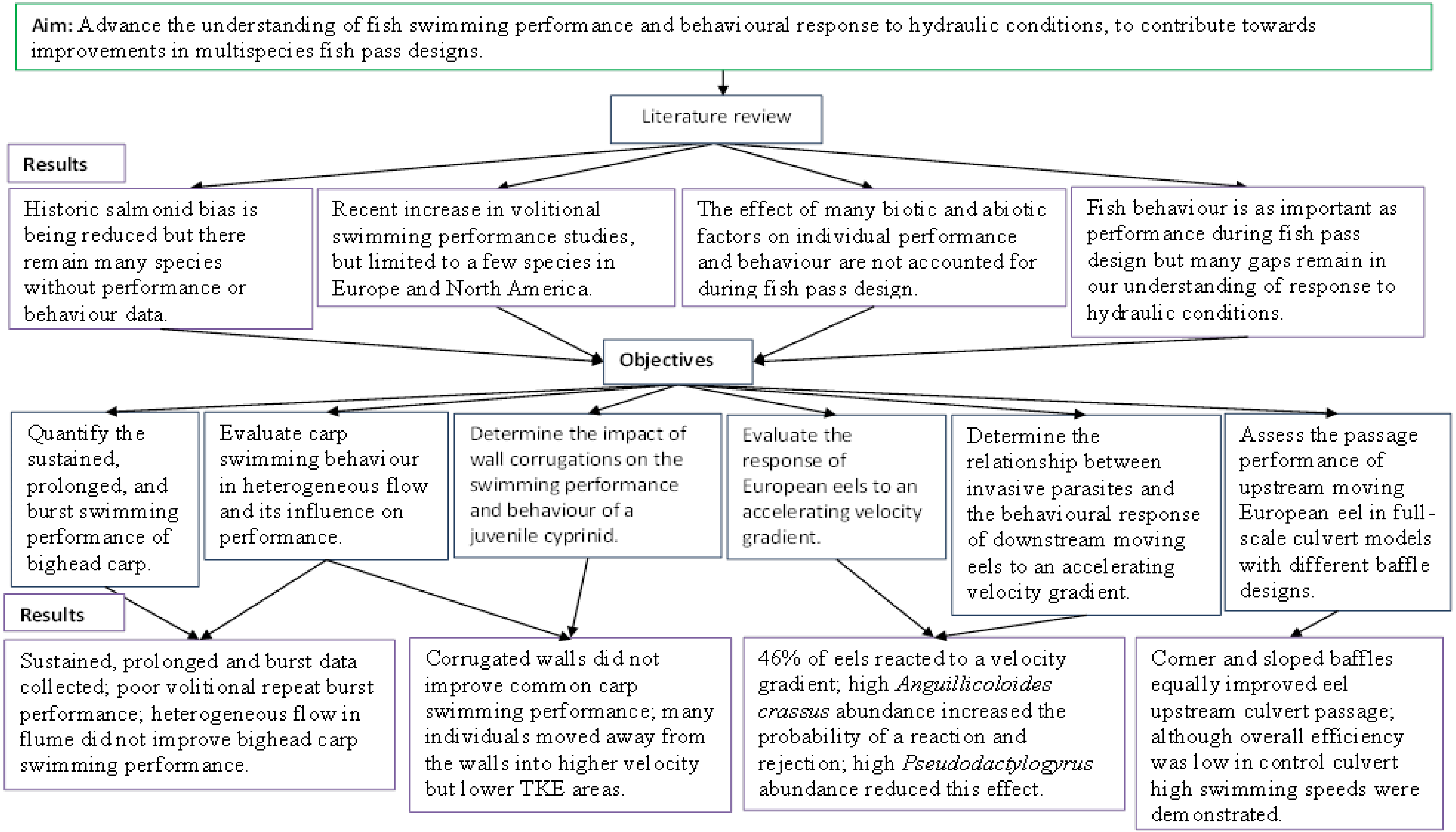
8.6. Conclusion

Improving accessibility to suitable habitat upstream of barriers will assist in recruitment and population recovery of the European eel (White and Knights, 1997; Briand *et al*., 2005; Laffaille *et al*., 2009). Research has largely focused on improving upstream passage at dams and weirs as opposed to culverts (Feunteun, 2002). This study demonstrates that culverts with homogeneous flow and moderate water velocities can impede yellow eel movements. Where a new water crossing is required, a bridge or wide culvert with flow and substrate equal to local river conditions is recommended to encourage multi-species passage (Armstrong *et al*., 2010; Barnard *et al*., 2013). However, where this is not feasible, or where existing culverts block eel movement, corner baffle installation can reduce water velocities, therefore may allow access to upstream reaches. In addition, their current use for other species should also benefit yellow eel habitat access. Furthermore, the encouraging results described for the prototype sloped baffles justify further research and development. Evaluation of multi life stages including elver passage, hydraulic conditions, and debris transport at a range of culvert slopes, lengths, and flows is recommended to optimise the design. For migrating fish in their natural environment, the benefits of baffles may be even more pronounced, due to the strong desire to progress upstream, and field tests should be conducted to confirm eel behaviour and passage performance in situ.

Chapter 9: Thesis Discussion

9.1. Introduction

Anthropogenic barriers to fish migration are contributing to the decline of many fish species worldwide (Lucas and Baras, 2001; Marmulla, 2001), yet current fish pass facilities are often ineffective (Bunt *et al.*, 2012; Noonan *et al.*, 2012). Efforts to improve passage must include consideration of the native fish species swimming ability and behaviour (Castro-Santos and Haro, 2006; Williams *et al.*, 2012). Due to the historic bias towards salmonid fish passes, this thesis focused on better understanding the performance and behaviour of non-salmonid species with different body morphologies and life histories. Figure 9.1 summarises how the aim and objectives were met and the key findings of each results chapter. The remainder of this chapter discusses these results, firstly in terms of their contribution to advancing current knowledge of fish swimming performance and behaviour, then through recommendations for fish passage design and broader applications. In addition, limitations to the data and areas requiring further research are considered.



Aim: Advance the understanding of fish swimming performance and behavioural response to hydraulic conditions, to contribute towards improvements in multispecies fish pass designs.

Historic salmonid bias is being reduced but there remain many species without performance or behaviour data.

Recent increase in volitional swimming performance studies, but limited to a few species in Europe and North America.

The effect of many biotic and abiotic factors on individual performance and behaviour are not accounted for during fish pass design.

Fish behaviour is as important as performance during fish pass design but many gaps remain in our understanding of response to hydraulic conditions.

Quantify the sustained, prolonged, and burst swimming performance of bighead carp.

Evaluate carp swimming behaviour in heterogeneous flow and its influence on performance.

Determine the impact of wall corrugations on the swimming performance and behaviour of a juvenile cyprinid.

Evaluate the response of European eels to an accelerating velocity gradient.

Determine the relationship between invasive parasites and the behavioural response of downstream moving eels to an accelerating velocity gradient.

Assess the passage performance of upstream moving European eel in full-scale culvert models with different baffle designs.

Sustained, prolonged and burst data collected; poor volitional repeat burst performance; heterogeneous flow in flume did not improve bighead carp swimming performance.

Corrugated walls did not improve common carp swimming performance; many individuals moved away from the walls into higher velocity but lower TKE areas.

46% of eels reacted to a velocity gradient; high *Anguillicoloides crassus* abundance increased the probability of a reaction and rejection; high *Pseudodactylogyrus* abundance reduced this effect.

Corner and sloped baffles equally improved eel upstream culvert passage; although overall efficiency was low in control culvert high swimming speeds were demonstrated.

Figure 9.1. Schematic summary of the aim, objectives and results of this thesis.

9.2. Advancements in the field of fish swimming performance and behavioural response to hydraulic conditions

The literature review (Chapter 2) found that following criticism of swim chamber methods in the late 1990s and early 21st century (e.g. Peake, 2004a; Castro-Santos and Haro, 2008), swimming performance was increasingly evaluated using volitional open channel flume studies, particularly when the data were aimed at informing fish pass design criteria. This methodology allows fish to adopt performance enhancing behaviours (Peake and Farrell, 2004; Tudorache *et al.*, 2007) and facilitates the evaluation of behavioural influences on performance (Castro-Santos, 2005; 2006). Despite this, volitional performance data are still relatively limited in the range of species, life stages, and temperatures evaluated, compared to a long history of swim chamber research. Therefore, fish pass and culvert design velocities continue to be dominated by swimming ability data collected using swim chamber methods. This thesis included an evaluation of the volitional swimming performance of bighead carp (*Hypophthalmichthys nobilis*, Richardson 1845) and European eel (*Anguilla anguilla*, L. 1758), species of economic and conservation importance in China and Europe (Chapters 5 and 8, respectively).

During the study of eel passage through an experimental culvert (Chapter 8), it was confirmed that previous estimates of performance were conservative. Eel swim chamber burst swimming speeds are approximately 1.15 to 1.35 m s^{-1} for 20 to 60 cm fish (reviewed in: Solomon and Beach, 2004). Yet some yellow eels (37 – 49 cm *TL*) were able to ascend the unmodified culvert against water velocities greater than 1.50 m s^{-1}. However, there was no evidence of improved bighead carp swimming performance during volitional passage of three consecutive flume constrictions compared to that achieved in swim chamber fixed velocity tests (Chapter 5). Fish approximately 100 mm long reached burst speeds of up to 0.74 m s^{-1} in the fixed velocity tests. Based on their average ground speeds, fish that passed the small area of high velocity at each constriction, may have reached swimming speeds of 0.69 to 0.83 m s^{-1} (maximum water velocities = 0.50 and 0.57 m s^{-1} in low and high velocity treatments, respectively), however, most of the flume consisted of velocities lower than this. Yet not all individuals were able to pass the constrictions. Similar results were reported by Bestgen *et al*. (2010), who did not find a noticeable improvement in Rio Grande silvery minnow (*Hybognathus amarus*, Girard 1856) performance during volitional flume passage compared to an U_{crit} test. Behavioural motivation may have been a factor determining flume ascent of Rio Grande silvery minnow and bighead carp (Mallen-Cooper, 1992; Castro-Santos, 2005). However, much of the open channel volitional research has been conducted with large adult fish (e.g. Haro *et al.*, 2004; Castro-Santos, 2004; Russon and Kemp, 2011a) and more research with juveniles and small fish is merited. Furthermore, bighead carp flume ascent required passage of three high velocity areas, in contrast to a single burst of movement from a standing start in the swim chamber, an area of study that should be considered further during fish pass design.

During slow aerobic swimming, fish often employ a steady gait, with a change to burst-and-coast swimming as white muscles are recruited (Peake and Farrell, 2004). In the small area of a swim chamber, fish are unable to utilise this unsteady gait effectively (Tudorache *et al.*, 2007; Peake and Farrell, 2006), therefore, open channel flumes are preferable for quantifying burst swimming ability. However, swim chambers may be suitable for the evaluation of steady sustained swimming speeds. This suggestion is supported by the fixed velocity trials presented in Chapter 5. The relationship between bighead carp swimming speeds and endurance was highly variable at burst and prolonged speeds (regression R^2 values of 0.26 and 0.20, respectively) and fish were observed swimming erratically in the test section. Whereas at slow, sustained swimming speeds, fish swam steadily and there was less variation in the relationship between maximum sustained speed, body length and temperature (regression $R^2 = 0.72$). Due to the poor relationship between speed and endurance at anaerobic speeds, the management recommendations for velocity criteria were based on speeds exceeded by the majority of individuals, rather than using regression models to predict ability. The original intention was to then apply the relationship between speed and endurance to predict maximum distance of ascent dependent on water velocity and swimming speed selected, and to calculate optimum ground speeds. However, the highly variable data and unreliable regression models meant this was not a feasible approach in this study.

High individual variability in swimming performance is commonly reported in experimental research (Kolok, 1992; Castro-Santos, 2006; Marras *et al*., 2010). Indeed swimming performance variability was high for bighead carp of the same size and at the same water temperature; in addition to the variation in performance during fixed velocity trials, the speeds reached in constant acceleration tests by equally sized fish varied by 0.23 m s^{-1}, and only a proportion of individuals passed the flume constrictions. Passage success of velocity barriers is not a binary response as commonly portrayed, and instead a greater portion of individuals will pass as velocity or distance is reduced. These findings demonstrate that utilising mean performance when determining velocity criteria and predicting distance of ascent can lead to a partial barrier and only faster swimming individuals moving upstream (Jones *et al.*, 1974; Plaut, 2001; Larinier, 2002c). Attempts to account for this variability when setting velocity criteria for culverts and fish pass facilities, based on the percentage of a population able to pass (see Chapter 2; Haro *et al.*, 2004; Castro-Santos, 2006), should be expanded.

Many fish can utilise the lower velocities created at the substrate-water interface to save energy during upstream movement (Barbin and Krueger, 1994; Adams *et al.*, 2003; Standen *et al.*, 2004). Therefore, it has been suggested that weak swimming fish species should be able to ascend culverts against mid-channel velocities designed for stronger swimming species by using the low velocity zone (e.g. Scottish Executive, 2000). Others have suggested setting culvert velocity criteria for small fish based on low velocity areas rather than mean cross-sectional velocity (e.g. Ead *et al*., 2000; Clark *et al.*, 2014). This principle was not supported by the behavioural data collected for cyprinids or eels in this thesis. Use of low velocity areas may be influenced by other hydraulic factors such as mean channel velocity (Chapter 5), turbulence (Chapter 6) and water depth (Chapter 8). In Chapter 8, only one eel that successfully ascended the control culvert did so along the edge, the remainder swam either entirely or mostly in the centre of the barrel (Plate 9.1). Although the edge region had lower velocities it was also characterised by low water depth. Swimming at the culvert edge would have forced fish to swim near the air-water interface, thus increasing wave drag and potentially reducing swimming performance (Hertel, 1966; Webb *et al*., 1991; Hughs, 2004).

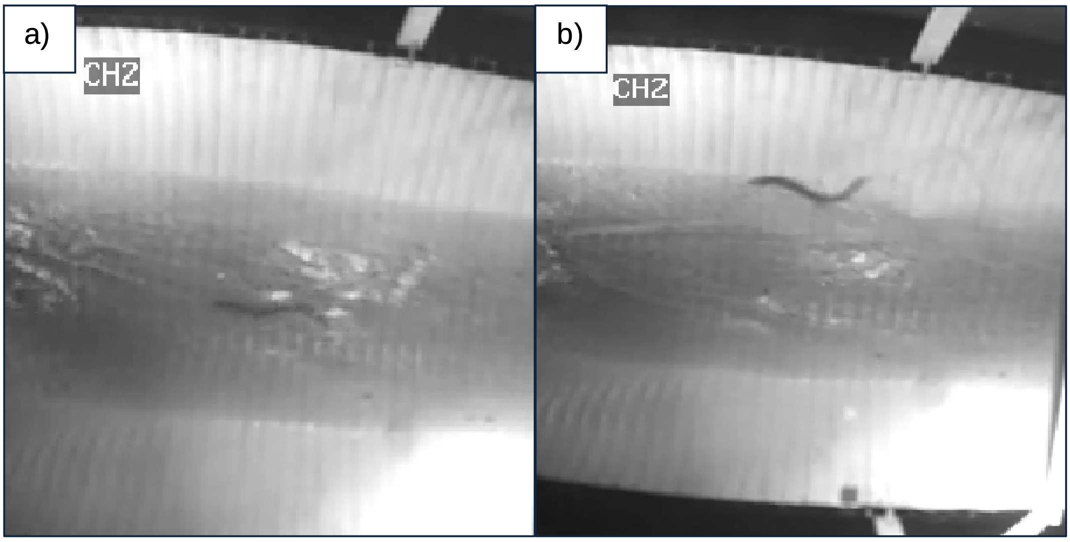


Plate 9.1. Adult European eel ascending an experimental culvert within an outdoor flume at the International Centre for Ecohydraulics Research, University of Southampton, against a mean channel velocity of 1.43 m s^{-1} either: a) along the culvert centre; or b) in shallow slower flowing water at the culvert edge.

During fixed velocity tests conducted in a section of open channel flume, bighead carp only swam close to the channel walls and floor when mid-channel velocity was within sustained swimming speeds, and moved into the flume centre at higher bulk flows (Chapter 5). During a recent experimental flume study, European eel were benthic oriented under control conditions, but when faced with high velocity and more turbulent streaming and plunging flow, movement into the middle of the water column was common (Piper, 2012). Therefore, it was hypothesised that turbulence may have incurred an energetic cost by forcing eels to swim in areas of higher water velocity. It is possible that turbulence induced by the flume’s hydraulic pumps destabilised bighead carp at high flows, however this was not evaluated so no firm conclusions can be drawn. Chapter 6 of this thesis presented the first detailed analysis of this type of behaviour, alongside evaluation of the hydraulic conditions experienced, with common carp (*Cyprinus carpio*, L. 1758). A link between fish passage of corrugated culverts and turbulence intensity in the low velocity area had been suggested by previous authors (Powers *et al.*, 1997; Kahler and Quinn, 1998), however the evidence was limited. Therefore, a fine scale tracking approach was utilised to evaluate fish movements, making it possible to better determine the relationships between turbulence, behaviour and performance. Occupation of low velocity areas was shown to depend on the size of corrugations and the hydraulic conditions induced. Fish did not always exploit the lower velocity areas created by larger corrugations, and instead often moved to areas of higher velocity and lower turbulent kinetic energy (TKE). Thus swimming performance was not improved by corrugated compared to smooth walls.

A change in rheotaxis and retreat upstream has previously been observed for salmonids encountering accelerating velocity gradients (e.g. Kemp *et al.*, 2005; Russon and Kemp, 2011b; Vowles *et al.*, 2014) and in Chapter 7 European eel were found to regularly exhibit the same behaviour. This avoidance behaviour was in contrast to behaviour at a shorter velocity gradient created by an orifice weir, where eels did not respond until contact with the structure (Russon and Kemp, 2011b). Therefore, further research into the specific hydraulic conditions that induce avoidance in European eel could lead to improved bypass designs. Eels with a high abundance of the invasive parasite, *Anguillicoloides crassus*, were also more likely to reject the velocity gradient and exhibit a longer passage delay. It is not possible to determine from Chapter 7 whether the high abundance of *A. crassus* was the cause of this reactive behaviour, or whether these fish had an inherent behavioural difference that led to a high parasite burden. To prove causality, a before and after type method would be required with experimentally infected fish. Regardless of causality, this research demonstrates a significant variation in behaviour and a link to fish health. Considering only healthy individual's behaviour, or using a mean value for hydraulic thresholds at which behavioural change occurs, could therefore disadvantage a proportion of the population.

The research presented in this thesis has contributed to the existing fish swimming performance and behaviour literature. Parts of this thesis are therefore published or under consideration for publication in high impact peer reviewed journals or have otherwise been presented to the international fisheries community:

- Parts of the literature review were adapted for a book chapter on ecohydraulics and fish pass design, highlighting the need to combine the expertise of fish biologists and engineers to create more effective fish passes based on realistic measures of swimming ability and behaviour: Vowles, A. S., Eakins, L. R.*, Piper, A.T., Kerr, J. R. & Kemp, P. S. (2013). Developing realistic fish passage criteria – An ecohydraulics approach. In *Ecohydraulics: An integrated approach*

(Maddock, I., Harby, A., Kemp, P. & Wood, P., eds.), pp 143-156, Wiley, Chichester. *Eakins is the maiden name of Lynda Newbold.

- The research presented in Chapter 5 is the first to utilise multiple methods to explore the swimming ability of bighead carp and to consider behaviour. The research has been presented to researchers at the Yichang University in China to inform future studies and will be submitted to the journal Acta Ecological Sinica.

- Chapter 6 presents the first fine scale evaluation of fish behaviour in the vicinity of corrugated walls. This study confirms the speculations by previous authors that turbulence created by corrugated culverts may inhibit the passage of small fish, and provides behavioural data to explain this response. This chapter is under review for publication in the journal Ecological Engineering.

- Chapter 7 presents the first data on the behaviour of European eels infected with the invasive parasites, *Anguillicoloides crassus* and *Pseudodactylogyrus* species. These findings were presented at the 2011 Fisheries Society of the British Isles (FSBI) symposia and is in press with the Journal of Fish Biology.

- The suitability of common culvert baffles for the European eel had not previously been tested, therefore, research was conducted to explore the suitability of a traditional corner baffle and prototype sloped baffle design for upstream moving eel (Chapter 8). This research is published as: Newbold, L. R., Karageorgopoulos, P. & Kemp, P. S. (2014). Corner and sloped culvert baffles improve the upstream passage of adult European eels (*Anguilla anguilla*). *Ecological Engineering*, **73**, 752-759.

9.3. Application to multispecies fish pass design

9.3.1. Fish passage design for Chinese cyprinids

In Chapter 5 a range of methods were used to study juvenile bighead carp swimming performance and behaviour, and provide initial water velocity criteria for fish passes. Where small fish 50 to 100 mm long are present it is recommended to keep short areas of high velocity at weirs and sluices below 0.60 m s^{-1}, and less than 0.50 m s^{-1} where multiple bursts or a longer distance (e.g. of 10 m or more) of high speed swimming is required. The swimming performance data collected can also be used for screening of intakes, where the approach velocity (velocity perpendicular to the screen face), is recommended not to exceed the predicted 90th percentile of sustained swimming speeds for the smallest fish present (Turnpenny and O'Keeffe, 2005), equivalent to 0.40 m s^{-1} for bighead carp. Based on behavioural data for bighead and common carp (Chapters 5 and 6), culvert and fish pass mid-channel velocity should be kept within swimming ability, rather than assuming occupation of lower velocity areas.

To accommodate multiple species, fish pass velocities should be suitable for the weakest swimming fish (FAO and DVWK, 2002). Grass carp (*Ctenopharyngodon idella*, Valenciennes 1844) (120-150 mm *FL*) have a critical swimming speed of approximately 0.70 m s^{-1} at 19 °C (Zhao and Han, 1980), which is within the same range as prolonged speeds for similar sized bighead carp (Chapter 5). Although it should be noted that the data for grass carp are based on few replicates. Silver carp (*Hypophthalmichthys molitrix*, Valenciennes 1844) have a weaker swimming performance in sustained, prolonged and burst modes than bighead carp during fixed velocity tests, but for juveniles 80 to 120 mm long this difference is minimal (Hoover *et al.*, 2012). Common carp white muscle recruitment begins at approximately 0.43 m s^{-1} for 110 to 140 mm fish at 20 °C (Rome *et al.*, 1990) and Tudorache *et al.* (2007) reported a gait transition speed (whereby anaerobic metabolism is assumed to begin) of approximately 0.45 m s^{-1} at 22 °C (*FL* = 100 to 200 mm). These results are similar to the bighead carp sustained swimming speeds (predicted mean = 0.47 m s^{-1} for 100 mm fish). Although the available data are limited, and caution is recommended for silver carp, this indicates that fish pass criteria based on juvenile bighead carp capability may be suitable for passage of other economically valuable Asian carp of a similar size.

Due to the bighead carp's relatively weak swimming performance and predominantly benthic oriented behaviour (Chapter 5) it is suggested that nature like and vertical slot type fish passes could be suitable for their upstream passage. If vertical slot passes are utilised they should have a lower head drop, velocities and turbulence levels than traditional temperate designs. In the UK, guidelines recommend a maximum velocity in pool and weir fish passes of 3 to 3.4 m s^{-1} for Atlantic salmon (*Salmo salar*, L. 1758) and 1.4 to 2 m s^{-1} for coarse fish (Armstrong *et al.*, 2010), both of which exceed the maximum speed recorded for bighead carp up to 0.22 m long (1.22 m s^{-1}). Nature like fish passes are becoming increasingly common in Europe, as they are used by a range of fish species (Jungwirth, 1996; Santos *et al.*, 2005; Calles and Greenberg, 2007) and passage efficiencies are generally between 50% and 100% (Bunt *et al.*, 2012). However, challenges remain in researching suitable layouts for the roughness elements and creating optimal hydraulic conditions (Katopodis *et al*., 2001). Furthermore, attraction efficiencies are often lower than for technical fish passes due to a limited discharge (Bunt *et al.*, 2012). It has also been suggested that the shallow water depth normally created may reduce attraction for species that inhabit large deep rivers without ascending smaller tributaries (Castro-Santos and Haro, 2006; Haro *et al.*, 2008), therefore, a variation on the European design may be required for Chinese carp.

Although nature like and vertical slot fish passes could be suitable for low to medium head structures disconnecting lakes from rivers in China, high head dams would require alternative solutions such as fish lifts (Travade and Larinier, 2002). Furthermore, on large rivers where dams can be hundreds of metres wide, a single fish pass will not be sufficient and two or more may be required (Clay, 1995). At all large dams on the Columbia River a collection gallery is included, with multiple entrances along the width of the powerhouse entering a channel connected to the fish pass (Clay, 1995; Fig 9.2). A similar solution is recommended for large rivers in China.

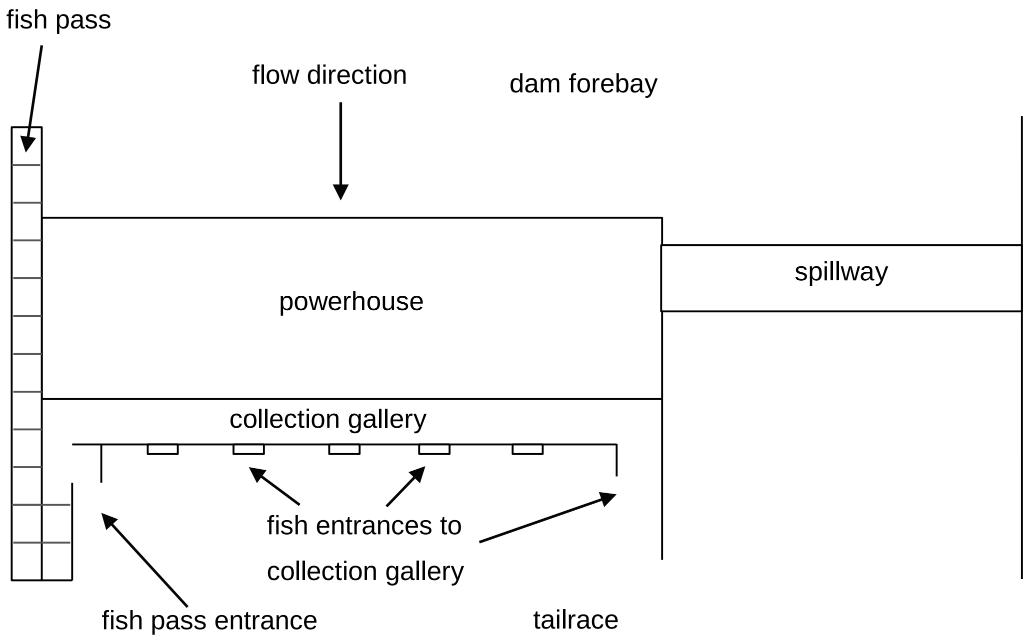


Figure 9.2. Diagram of a hydroelectric dam with collection gallery and pool and weir fish pass (adapted from FAO and DVWK, 2002).

Despite a resurgence in upstream fish passage design and installation in China since the beginning of the 21st century, without downstream bypass routes safe dispersal of fish may be restricted to one direction (Godinho and Kynard, 2009). There are currently no downstream bypasses in China and no published data on native species behaviour (e.g. reaction to velocity gradients, overhead cover, light, sound), which may influence downstream bypass efficiencies. Development of behavioural barriers to deflect carp from turbines and towards bypass systems in China can draw on global research to limit the spread of invasive Asian carp. In an attempt to prevent bighead and silver carp spreading along the Illinois River and into the Laurentian Great Lakes, there are three electric barriers in place, with ongoing efforts for improvement (Moy *et al.*, 2011). A Bioacoustic Fish Fence system (BAFF), formed from a bubble curtain combined with acoustic stimuli (Fish Guidance Systems Ltd., UK) was shown to deter 95% of 284 passage attempts made by bighead carp in an experimental raceway system (Taylor *et al.*, 2005). A similar solution could be an option in China as a behavioural deterrent for bighead carp approaching turbine intakes. In this instance deterrence would not need to be 100% effective to significantly improve survival, in contrast to the aim of completely excluding Asian carp from sensitive ecosystems in the USA.

9.3.2. Fish pass design for the European eel

This thesis supports recent volitional data from another study (Russon and Kemp, 2011a) that suggests the current velocity criteria for eels may be conservative (Chapter 8). Swimming speeds greater than 1.50 m s^{-1} and potentially as high as 2.29 m s^{-1} (based on mean culvert velocity and passage time) were observed for yellow eels. The speeds observed in this study are comparable to the results of Russon and Kemp (2011a) who observed larger silver eels passing water velocities of 1.75 to 2.12 m s^{-1} over a distance of approximately 1 m. Recent evaluation of yellow eel passage over an experimental gauging weir also found that a small percentage were able to pass when velocity at the bottom of the weir slope was 2.43 m s^{-1} (J. Kerr, pers. comm.). However, in both the research presented by Russon and Kemp (2011a) and during this thesis, the high speeds were reached when turbulence was low. Furthermore, although all silver eels were able to pass a short area of high velocity created by an undershot weir (Russon and Kemp, 2011a), only a small proportion (28%) were able to pass the culvert tested in Chapter 8, at lower velocities but over a greater distance. Therefore, such high velocities over more than a very short distance could create a selective barrier only passable to the strongest swimming individuals, or only during temporal changes in flow conditions (Lucas *et al.*, 2009). In upper river reaches where yellow eels conduct random movements for dispersal (Ibbotson *et al.*, 2002) a partial barrier may be acceptable. However, in lower river reaches, where smaller eels are more likely (White and Knights, 1997) and upstream movement is needed to reach suitable habitats and reduce downstream densities, velocities this high would not be recommended.

According to the Environment Agency's NFCDD database there are 12,000 culverted channels in England and Wales. It is not possible to determine the proportion of these that are pipe or box culverts under infrastructure, as opposed to concreted channels through urbanised areas, as both are labelled identically. However, culverts are certainly found in high densities across the UK. Chapter 8 provides the first data on eel passage efficiency through a pipe culvert with different baffle designs. Both corner baffles, currently utilised for other fish species, and prototype sloped baffles are recommended to facilitate upstream movement of yellow eels where culvert velocity is high. However, eels occasionally contacted the flume constriction used in Chapter 7 and reacted by startling upstream; a similar behaviour upon reaching the baffles in the culvert could have contributed to the high number of retreats back downstream, delaying ascent. This reaction to physical structures has also been observed for eels contacting bar screens and weirs (Adam *et al.*, 1999; Russon *et al.*, 2010; Russon and Kemp, 2011b). Baffle designs should encourage eels to continue quickly upstream, rather than congregate downstream where predation risk would be enhanced (Lang *et al.*, 2004). It is therefore suggested not to use baffles that cross the full culvert cross section if eels are present, until further behavioural research has been conducted. Small spoiler baffles may be suitable for eel passage and have been used to successfully restore movement of weak swimming inanga (*Galaxias maculatus*, Jenyns 1842) (Franklin and Bartels, 2012) in New Zealand and inanga and spotted galaxius (*Galaxias truttaceus*, Valenciennes 1846) in Australia (MacDonald and Davies, 2007). This type of relatively small baffle can be used to create low velocity resting areas (Feurich *et al.*, 2011) and would limit the effect on culvert discharge capacity (Rajaratnam *et al.*, 1990; Feurich *et al.*, 2011). Based on the findings of Chapter 6 (albeit on common carp), the influence of corrugated culvert surfaces on eel passage should also be considered, due to potential impacts of turbulence on behaviour and passage.

The effect of turbulence on eel swimming ability and behaviour remains an area requiring further study. Passage efficiency of European eel at an intertidal weir was twofold higher with plunging than streaming flow (Piper *et al.*, 2012), potentially due to the turbulence created acting as a navigational aid (Clay, 1995). However, during an experimental study, although attraction was high, passage rates were lower in turbulent plunging and streaming flow than control conditions (Piper, 2012). The higher turbulent kinetic energy (TKE) created by sloped baffles compared to corner baffles in Chapter 8 did not appear to negatively affect eel passage through the culvert. Passage delay and entry rate were however both higher with sloped baffles as eels retreated downstream multiple times before culvert ascent. Although this was not statistically significant and may reflect random variation, it is possible that reluctance to pass the area of high TKE and velocity contributed to delayed passage. It is recommended to test sloped baffles in a longer culvert and at a higher discharge, as the cumulative energetic costs of passing a large number of baffles could influence success.

Hydropower dams can severely deplete the proportion of eels reaching the ocean (Calles *et al.*, 2010; Pedersen *et al.*, 2012) and it is essential that efficient bypasses are installed. For example, there was a 58% loss of silver eels during downstream migration at the Tange hydropower plant on the River Gudena, Denmark (Pedersen *et al*., 2012). Despite a common belief that eels move passively downstream following the main current (Porcher, 2002; Tesch, 2003), they have been observed to show milling and retreating behaviour at dams (e.g. Haro *et al*., 2000a; Jansen *et al*., 2007; Brujis and Durif, 2009). Chapter 7 illustrates that on a fine scale, eel behaviour can be influenced by hydraulic stimuli. In this study 46% of silver eels reacted to a velocity gradient and 36% rejected the constricted channel, causing delay in downstream passage. Based on the high proportion of eels reacting to the velocity gradient, a smooth, gently accelerating flow at the bypass entrance is recommended, as has been for other fish species (Turnpenny and O'Keeffe, 2005; Environment Agency, 2011b).

In a recent field study the velocity at which eels responded to accelerating flow varied between treatments, but the spatial velocity gradient over two body lengths was not statistically different (Piper, 2012). This observation suggests that eels may respond to velocity acceleration at thresholds values, in a similar way to that observed for salmonids (Enders *et al.*, 2009; Russon and Kemp, 2011b; Vowles and Kemp, 2012). In the experimental study presented in this thesis only one flow condition was tested and the reaction occurred at variable locations. This variation in behaviour was partly due to individuals moving downstream tail first reacting sooner than those moving head first. However, fish swimming under the same rheotaxis also showed high variability in the location of response. Understanding this avoidance behaviour could improve bypass designs.

In Chapter 7 it was demonstrated that eels heavily infected with the invasive swim bladder parasite *Anguillicoloides crassus* were more likely to avoid accelerating velocity, with the potential for delayed passage at anthropogenic structures. This parasite may also affect fish passage of weirs and culverts, where a partial barrier to migration may be created for infected fish with a reduced swimming ability. However, there is some inconsistency in the results of studies exploring the effect of *A. crassus* on swimming ability. Although some have observed a negative impact (Sprengel and

Luchtenberg, 1991; Palstra *et al.* 2007), the maximum swimming speed of glass eels was not influenced by *A. crassus* (Nimeth *et al*., 2000) and there was no difference between the endurance of infected and control yellow eels (Münderle *et al*., 2004). It is possible that the results are influenced by the eel life stage; the only study with silver eels, prior to the current research, found significantly more fish fatiguing in a U_{crit} test before 0.7 m s^{-1} and a higher cost of transport in infected eels (Palstra *et al.*, 2007). Further research into the influence of *A. crassus* should consider volitional swimming ability and the effect of current and historic parasite infection on performance and behaviour.

9.4. Further applications: Predicting habitat occupation, range expansions and barrier passability

Fish's natural behavioural response to hydraulic conditions is based on the need to maximise fitness, by minimising the risk of predation and cost of locomotion, whilst maximising energetic inputs from feeding (Trump and Legget, 1980; Bernatchez and Dodson, 1987; Nislow *et al*., 1999; Railsback *et al*., 1999; McElroy *et al*. 2012). Behaviours commonly observed in the laboratory, such as avoidance of accelerating flow and occupation of low turbulent conditions are based on the natural response in situ to meet these fitness requirements (Nestler *et al*., 2008). Understanding swimming ability and behaviour can therefore increase our understanding of fish movements and habitat use in the wild (Booker, 2003; Kodric-Brown and Nicoletto, 2005). On a reach scale, ability to withstand high velocities and behavioural preferences for different hydraulic conditions can determine the segregation of multiple species into separate microhabitats (Peak *et al*., 1997a; Fulton *et al*., 2000). For example, juvenile Atlantic salmon (*Salmo salar*, L. 1758) and brook trout (*Salvelinus fontinalis*, Mitchill 1814) have similar food intake requirements, but Atlantic salmon parr have a greater swimming ability, therefore, segregation of feeding habitats likely depends at least partially on river velocities (Peake *et al*., 1997a).

Swimming performance data can be used to predict changes in species composition within habitat patches and river reaches based on management decisions. For example, modification of the river channel through straightening, bank modification, and concreting, can result in higher water velocities than in a natural channel, and a loss of low velocity refuge areas (Cowx and Welcomme, 1998). This can reduce the carrying capacity of modified reaches for weak swimming species, particularly during high discharge events when swimming ability is exceeded throughout the channel (Cowx and Welcomme, 1998; Booker, 2003). However, swimming ability alone does not determine susceptibility to downstream displacement during floods. Displacement is also influenced by behavioural adaptations such as oral grasping onto the substrate, and the ability to locate and utilise small patches of low velocity (Scott and Magoulick, 2008; Leavy and Bonner, 2009). The data collected in this thesis contributes to our understanding of carp and eel behaviour in various hydraulic conditions, and their potential response to altered flows.

Habitat modelling to predict the presence or absence of various fish species is largely based on evaluations of water velocity, depth, and substrate (Mouton *et al.*, 2007). However, recent research suggests that turbulence may also be an important contributor to energetic costs of fish swimming, and therefore to habitat use, at least on the micro scale (Cotel *et al.*, 2006; Smith *et al.*, 2006; Wilkes *et al.*, 2013; Chapter 6). For example, Cotel *et al.* (2006) showed that brown trout selected resting areas with lower turbulence intensity than similar unoccupied areas (within substratum dips where large woody debris was present). Flume based research, such as that presented in Chapter 6 with common carp, allows the individual movements of fish to be tracked and related to hydraulic conditions, to increase our understanding of potential habitat selection processes. This thesis shows that, similar to the trout studied by Cotel *et al.* (2006), common carp selected areas of lower intensities of turbulence without moving into mid-channel flow (Chapter 6). Initial flume based research followed by validation in the field is essential to ensuring habitat models are based on realistic behavioural decisions rather than simplistic assumptions. Research to date is limited and considerably more data at a range of flow conditions and for additional non-salmonid species is needed before turbulence can be included in habitat management guidance (Wilkes *et al.*, 2013). As well as providing species specific data, the observations on common and bighead carp (Chapter 5 and 6) enhance our understanding of how a range of species use low velocity areas and react to turbulence zones, to move towards a better overall understanding of fish behaviour.

Knowledge of fish swimming ability and behaviour can also be used to understand the spread of invasive species and their ability to outcompete native fish. For example, invasive rainbow trout (*Oncorhynchus mykiss,* Walbaum 1792) in western North America and hybrids between rainbow and native Yellowstone cutthroat trout (*O. clarkii bouvieri*, Richardson 1836) have a better swimming performance than the native species, thus suggesting outcompeting may occur (Seiler and Keeley, 2007). As there is very little data available on bighead carp swimming performance and behaviour, the data collected in Chapter 5 has the potential to contribute towards understanding their range expansion and competition with native species. In addition, this data can also be utilised to create barriers to the spread of invasive fish (e.g. Neary *et al*., 2012; Noatch and Suski, 2012). Water velocities greater than the highest swimming speeds recorded (1.3 m s^{-1} for bighead carp < 25 cm) could be used to decrease the risk of some fish passing a barrier. In a similar study, Hoover *et al*. (2003) evaluated round goby (*Neogobius melanostomus*, Pallas 1814) swimming performance over various substrates and concluded that hydraulic barriers could limit their spread, but that rough substrates would require higher velocities for exclusion than in smooth channels. This was due to the goby’s ability to utilise the lower water velocity created at the rough boundary layer, thus demonstrating the importance of evaluating hydraulic conditions and swimming behaviour across the channel. The results presented in Chapters 5 and 6 for bighead and common carp, which showed movement away from the flume walls at high velocity (Chapter 5) and turbulence (Chapter 6), suggest that this may not be true for all species. Instead, it may be possible to use high velocity turbulent flow to deter Asian carp.

Although restoring habitat connectivity is often the most effective method of increasing native fish species diversity and abundance (Roni *et al*., 2002; 2008), installing a fish pass or removing a barrier has a high economic cost. For example, the Environment Agency estimated the cost of installing a vertical slot fish pass (head height >1.5 m) in England or Wales as £350,000-500,000 with an additional £30,000-60,000 of project management costs (Environment Agency, 2010). Therefore, with limited resources available and thousands of potential barriers to fish movements, it is essential to prioritise mitigation actions to ensure fish passes are installed where the biggest gains can be made to fish productivity (Kemp and O’Hanley, 2010). As the first stage of this process, a number of methods have been developed to assess the passability of individual structures, to determine which are full and partial barriers to fish movements (reviewed in Kemp and O'Hanley, 2010). Although the most accurate approach is to directly evaluate passage of fish using tracking techniques (e.g. PIT tags, radio-telemetry, acoustic telemetry), this is expensive and impossible to replicate at every barrier within a catchment. Therefore, several rule based methods have been developed which use barrier dimensions and hydraulic conditions, combined with fish swimming and leaping ability to predict passability across a large number of barriers without the need for extensive field data (e.g. Love and Taylor, 2003; Meixler *et al*., 2009; SNIFFER, 2010).

Rule based passability methods primarily depend on whether a height, velocity, or depth barrier to fish movements is presented by a structure. To determine whether a velocity barrier is present a good knowledge of the target species swimming ability is required. However, as shown in Chapter 2, most of the data available on which to base rules for passage success are based on swim chamber estimates of performance, which may be conservative. Conversely, turbulent flow may reduce passability by reducing swimming performance (e.g. Enders *et al*., 2005; Tritico and Cotel, 2010). More volitional studies of fish swimming performance in a range of hydraulic conditions are therefore needed to improve passability estimates.

Swimming ability depends on species (Katapodis and Gervais, 2012) and fish size (Bainbridge, 1958), and the effect of structures on different fish species can vary greatly (Ovidio and Philippart, 2002; MacPherson *et al*., 2012). Therefore, the differentiation between life stages and species with relatively high (e.g. salmonids: Peake *et al*., 1997) and low (e.g. lamprey and eels: Russon and Kemp, 2011; Chapter 8) maximum swimming speeds during a barrier passability assessment process is important when considering habitat management for the full fish community. Yet few current methods account for multiple species, and even fewer consider downstream movements (Kemp and O'Hanley, 2010), with most focusing on upstream moving salmonids (e.g. Taylor and Love, 2003; WDFW, 2009; Gargan *et al*., 2011). A much better understanding of multi-species swimming ability is still needed (Chapter 2) if the impact of barriers on the full fish community is to be assessed. Furthermore, behavioural responses are normally unaccounted for in barrier passability assessments (Kemp and O'Hanley, 2010), but as shown in this thesis (Chapter, 5, 6, 7), and other recent studies (e.g.

Vowles and Kemp, 2012; Piper, 2012), can strongly influence passage of anthropogenic structures.

Slight alterations in passability criteria and inconsistencies between the predicted and actual passability can lead to sub-optimal management decisions (Burford *et al*., 2009; Mahlum *et al*., 2014). Therefore, to optimise barrier removal or repair a good understanding of multi-species swimming ability and behaviour is required. This thesis contributes towards this through realistic assessment of European eel swimming performance and increasing our understanding of how cross sectional flow heterogeneity, turbulence, and accelerating velocity can influence fish behaviour and passage performance.

9.5. Research limitations and recommendations for further study

The initial results presented within this thesis provide a good indication of bighead carp swimming ability and can form a platform for further research. Further trials should be completed at high velocities in open channel flumes, and include larger fish and adults. In addition, it is important that the results are verified with wild fish. Hatcheries are generally very simple environments with little sensory stimuli, a ready supply of food, high densities of fish and no predators. Rearing in these conditions can lead to behavioural, developmental, biomechanical, and physiological differences to wild stock, and natural selection within hatcheries combined with broodstock selection for specific traits can lead to genetic change (Jonsson and Jonsson, 2006; Chittenden *et al*., 2010). Several studies have shown that the lack of high current velocities within hatchery conditions and fish’s limited exercise can result in hatchery reared individuals having a poorer swimming performance than those reared in the wild (e.g. McDonald *et al*. 1998; Ward and Hilwig 2004; Basaran *et al*., 2007; Pedersen *et al*., 2008; Chittenden et al., 2010). As wild bighead carp could not be obtained during this research, the next step should be to compare wild and hatchery performance to further inform the recoomendations put forward in this thesis.

When evaluating the behavioural response of fish to hydraulic conditions, many laboratory studies have used hatchery reared fish (e.g. turbulence, Smith *et al*., 2005; Liao, 2006; velocity gradients, Russon and Kemp, 2011b; Vowles *et al*., 2014). It is assumed that the behaviour exhibited by hatchery individuals will be similar to wild fish, although potentially with lower reaction thresholds (Vowles and Kemp, 2012). This is true for brown trout's behavioural response to threshold velocity gradients (Russon and Kemp, 2011; Vowles and Kemp, 2012). Enders *et al*. (2004) compared the costs of swimming in flow with different intensities of turbulence for wild, hatchery (1st generation from wild progeny), and domesticated (7th generation progeny) juvenile Atlantic salmon. They found that the cost of swimming in turbulent flow was greater for domesticated fish, potentially due to body morphology. However, instability (Tritico and Cotel, 2010) and increased energetic costs of swimming (Enders *et al*., 2005), from turbulent flow will apply to all fish regardless of their rearing conditions. Therefore, although the threshold at which avoidance or attraction to turbulent flow begins may differ, wild and hatchery reared fish will likely exhibit the same behavioural trends.

It is possible that wild bighead carp movement away from the flume wall at high velocities (Chapter 5) would have begun to occur at a higher threshold velocity than for the hatchery reared individuals used, but it is likely that behaviour would still change above sustained swimming speeds. Similarly, if wild common carp had been studied in Chapter 6 they may have moved away from the corrugated walls at a higher TKE. However, the trade-offs fish had to assess when selecting swimming location would be similar and trends between the four treatments should be realistic for wild fish. It is recommended to continue this research by evaluating behaviour at a range of discharge conditions, and concurrent validation with wild fish would ensure that the observations are transferable.

Many fish species are known to gain an energetic advantage from swimming in schools (e.g. Ross *et al*., 1992; Burgerhout *et al*., 2013). In addition, fish swimming in schools can learn from more experienced individuals, for example by transmitting novel foraging information amongst the group (Lachlan *et al*., 1998; Swaney *et al*., 2001). Anthropogenic structures may cause groups to break up, with some individuals passing the barrier first, and consequently losing the benefits of the school (Kemp *et al*., 2006). Migrating American shad are particularly unwilling to break school integrity, therefore, fish pass and bypass designs that enable groups to enter together may be more effective (Haro *et al*., 1998; Haro and Castro-Santos, 2012). Although they do not form close schools, silver eels move downstream in large groups (Brujis and Durif, 2009). It is unknown whether their behavioural response to hydraulic cues will differ in groups compared to trials using single individuals (e.g. Chapter 7). Further studies to evaluate the avoidance response of eels to different velocity gradients and attempts to improve bypass entrance designs could therefore benefit from including groups of fish. Yellow eel upstream migration is a random dispersal process conducted by individuals (Ibbotson *et al*., 2002); therefore the use of single fish in chapter 8 is unlikely to have influenced their behaviour. However, an important area of research to follow on from this study is the evaluation of elver passage through baffled culverts; a life-stage that does move upstream in large groups.

A key limitation of flume based research is the scale and simplicity of conditions compared to those available in the field (Rice *et al*., 2010). Although fish pass facilities and culverts are more similar to flume conditions than natural rivers are, the scale and complexity can still be much greater (Chapter 2). In this thesis only three constrictions were used to test the multiple burst performance of bighead carp (Chapter 5). As the proportion of fish passing upstream decreased at each constriction, the implications for passage of vertical slot fish passes with hundreds of pools could be considerable. In order to assess this accurately, wild migrating fish should be tagged and tracked through fish passes in situ. PIT tags can be used to evaluate individual ascent of fish passes, either with passage recorded at the entrance and exit, or at several locations within the pass to better understand reasons for fallback or passage success (Calles and Greenberg, 2007; Moser *et al*., 2011).

It is difficult to determine from flume based studies of avoidance behaviour and delayed passage whether this will have a significant biological effect in reality. Smooth channelled rectangular flumes provide little hydraulic diversity or cover upstream of the area of study, and fish typically move downstream through constricted areas within an hour, and often in only a few minutes (Haro *et al*., 1998; Kemp *et al*., 2006; Vowles and Kemp, 2012, Chapter 7). This makes proving an energetic cost of delay significant to migration success impossible. Delay in the field upstream of barriers can be several hours, days or weeks, and can include retreat upstream by several kilometres (Jansen *et al*., 2007; Pedersen *et al*., 2012). Therefore, flume based studies must be conducted alongside detailed field studies to assess the causes and extent of delay. An important area of future research for silver eel migrations is to quantify what effect delay at hydraulic barriers has on eel fitness.

To progress multi-species fish pass designs a combination of laboratory and field based research is required. A mix of volitional and forced swimming performance protocols can result in a comprehensive understanding of swimming ability. This should be followed by behavioural evaluation as there is clearly considerable scope for utilising natural fish behaviours to improve attraction to fish passes, minimise delay and enhance repellence from turbines. Field validation must then determine whether responses observed in the laboratory apply in more complex conditions (e.g. dam forebays). This transfer is now beginning to occur (e.g. overhead cover: Greenberg *et al*., 2012; bar rack angle: Calles *et al*., 2013), but more projects are needed to improve our understanding and lead to behavioural elements being widely accounted for in fish pass designs.

Chapter 10: Concluding remarks

Dams, weirs, sluices and culverts contribute to the fragmentation of freshwater habitat, reducing connectivity between fish populations and preventing or limiting the migrations of many species. These structures continue to be constructed globally, providing social and economic benefits. When generating renewable hydroelectricity, dams can also provide environmental benefits through a reduced dependence on energy sources such as coal and oil. Hydropower accounts for 85% of global renewable energy (Paish, 2002; IEA, 2012) and over 16% of all electricity production (IEA, 2012). In developing countries, including China, hydropower expansion continues with the construction of large dams. This development must be met with improved multispecies fish pass designs to maintain ecological connectivity and the productivity of fish species of conservation and economic importance. In Europe, small scale (< 10 MW installed capacity) hydropower schemes are increasingly being adopted due to technological advancements and financial incentives (Paish, 2002; Department of Energy and Climate Change, 2010). Therefore, in the UK, where historic low head weirs block fish movements, hydropower development is being advocated as a win-win solution, whereby renewable energy is supplied alongside the installation of a fish pass to meet the legislative requirements of developments (Environment Agency, 2010). However, such solutions can only be achieved if fish pass efficiencies are high enough to maintain sustainable populations.

Following the installation of new fish passes, monitoring should be conducted to provide data for iterative improvement. Post project monitoring is an area commonly understudied in river restoration projects (Bernhardt *et al*., 2007), including after fish pass installation (reviewed in: Roscoe and Hinch, 2010). In China, only one fish pass (the Yangtang fish pass on the Mishui River) has been evaluated to date (J. Tao, pers. comm.). As the swimming ability and behavioural data for most Chinese fish species is minimal, monitoring should occur alongside further experimental research to ensure that designs are optimised.

The experimental evaluation of swimming performance and behaviour, as presented in this thesis, is crucial to the design of fish passes that facilitate passage with minimal delay and energetic expense. However, basic swimming performance data are still required for many fish species. Flume based studies of high speed swimming are likely to be more realistic than those conducted in swim chambers. The latter are suitable for the evaluation of aerobic swimming speeds that can be maintained over longer distances, for application to fish pass pool and screen approach velocities. The historic literature is dominated by swim chamber research which continues to be utilised as a cheaper alternative to flume studies. Therefore, the relationship between chamber based performance and volitional swimming speeds should be explored. This thesis also demonstrated that turbulent flow in low velocity edge areas can influence fish behaviour. The effect of turbulence intensity and scale on passage success is an area still requiring considerable research and presents an important challenge to the design of multispecies fish pass facilities.

Historically fish’s behavioural response to hydraulic conditions was largely ignored in the design of passage facilities. This thesis clearly demonstrates the importance of behavioural response to velocity heterogeneity, turbulence and accelerating velocity on passage success and delay. Although many advancements have been made in understanding conditions that induce avoidance and attraction to fish pass facilities (e.g. Goodwin *et al.*, 2006; Enders *et al.*, 2009; Silva *et al.*, 2012a), further research is still required in a number of areas, which should utilise a range of species and hydraulic conditions. Furthermore, the mounting evidence on how fish respond to hydraulic cues must be transferred to more effective designs through collaborative work between ecologists and engineers. Finally, the potential for fish health to influence behaviour at anthropogenic structures is revealed in this thesis, a previously unstudied factor which could affect the quality and quantity of fish arriving at spawning grounds. Accounting for fish health adds additional complexity into the already challenging subject of improving fish pass efficiencies. However, a more comprehensive understanding of the mechanisms determining fish’s behavioural response to hydraulic stimuli could ultimately lead to improved fish pass designs.

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