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Aggregation in riverine fish: a review from a fish passage perspective

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Abstract According to the most recent Living Planet Report, freshwater fish species are among the most threatened species on Earth, with many of them showing a decline in population due to altered river connectivity caused by barriers. Fish passages are conservation measures aimed at mitigating the impact of such obstructions for migrating freshwater fish, providing corridors that should not harm, kill, stress, or excessively delay fish movement. Fish passage efficiency, however, is highly variable and often unknown, particularly for non-salmonids. Despite many species being gregarious, research aiming at assessing and improving passage efficiency has focused almost solely on behaviour and swimming performance of individual fish. Collective behaviour can, in fact, affect the way fish approach, enter, and pass a fishway. The mechanisms for which group behaviour affects fish movement in hydrodynamically complex environments, such as those occurring within fish passages, are multiple and not limited to: reduced energy expenditure, better navigation, reduced stress levels, increased exploratory behaviour, and change of predation dynamics. In this work, we review current research to illustrate how collective behaviour can be relevant for fish passage research. Our aim is to provide an overview of how collective behaviour might affect fish passage efficiency and how future research could improve fish passage design.

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1. Introduction

The loss of biodiversity caused by climate change and other anthropogenic activities is among the most concerning environmental issues of our time. The estimated rate at which species go extinct is so fast that the scientific community warns that a sixth mass extinction is ongoing (Ceballos et al., 2015). Freshwater ecosystems are vital for global biodiversity, hosting approximately 10% of the total known species and one-third of all vertebrate species, despite occupying less than 1% of Earth's surface (Strayer & Dudgeon, 2010). They also constitute vulnerable ecosystems, as freshwater species are those showing the most dramatic population decline. Migrating freshwater fishes represent an emblematic example of such loss, with a reported global decline of about 76% in abundance from 1970 to 2016 (Deinet et al., 2020).

Migrating fish regularly move along rivers for their survival. Reproduction, foraging, hiding, and resting require different environments and resources (Northcote, 1978). As a result, river fragmentation caused by dams, weirs, and culverts represents a tremendous challenge for migratory fish, and the increasing number of obstructions has been recognised as a critical driver for population decline. A survey conducted for 290 species found that habitat loss and degradation, particularly barriers to migration routes, represented the major threat (Deinet et al., 2020).

Dams are constructed for various purposes, such as flood control, water supply, recreation, navigation, and electricity generation (Zarfl et al., 2015), and over the last century, the number of barriers in rivers has increased. A study by Grill et al. (2019) shows that only 37% of the global rivers longer than 1 000 km remain free-flowing over their entire length. Artificial impoundments larger than 100 m² worldwide are estimated to be around 16.7 million, and this number is expected to increase (Lehner et al., 2011). Although in some cases these structures are obsolete and removable (Birnie-Gauvin et al., 2018; Gough et al., 2018; Watson et al., 2018), many will likely have to remain in place to play a role in both climate change mitigation and adaptation (Berga, 2016). Dams can, in fact, store water during times of drought (López-Moreno et al., 2009), regulate water flow to prevent flooding (Dixit, 2003), and generate renewable energy through hydropower, which can help reduce reliance on fossil fuels and mitigate climate change impacts (Edenhofer et al., 2011). As a result, migrating fish need to be supplied with a route for passing these barriers.

Fish passes - also referred to as *fishways* or *fish passages*- are artificial structures that provide a corridor for fish to safely overcome an anthropogenic obstacle along the river. They are built by opening an alternative waterway in the river and can be either built as concrete structures or nature-like (Katopodis et al., 2001; Larinier, 2002). Overall, the goal of every fish pass is to promote *safe and timely* fish movement across a barrier. A fishway should not substantially alter a fish's typical migration and life cycle: it should

not cause excessive delay, stress, injuries and - obviously – mortality (Roscoe & Hinch, 2010).

Even though much work on fish passes has focused on designing principles (Castro-Santos, 2005; Clay, 1995; Ead et al., 2004; Katopodis et al., 2001; Katopodis & Williams, 2012; Larinier, 2002; Odeh, 1999; Quaranta et al., 2019; Silva et al., 2018), information regarding their effectiveness, once they are in place, is not as exhaustive. In fact, in contrast with the increasing number of fish passages constructed worldwide, a relatively small proportion has an integrated monitoring system to assess passage efficiency (Noonan et al., 2012a). At many sites where assessments have been conducted, efficiency is relatively poor, especially for non-salmonid species (~60% vs ~25%) (Bunt et al., 2012; Noonan et al., 2012b).

The variable functionality of fishways highlights the need for new research-based solutions and approaches to mitigate the effects of barriers on migration. This is no trivial work: fishways must attract fish to their entrance, induce them to access and pass through and provide them with all conditions to do so without harm or delay (Castro-Santos et al., 2009). This implies that fishway design should involve different aspects related to behaviour and locomotion. Among these, collective behaviour has been almost entirely neglected in investigations concerning fish passage, while it could represent a relevant aspect to consider when targeting gregarious species.

In this work, we illustrate why and how aggregation can be relevant in relation to fish passage. Additionally, we advance some reflections on how this aspect can be integrated into future research.

2. Collective behaviour in hydrodynamically complex environments

Living and moving in a group can bring multiple benefits, such as reduced energy cost of movement, reduced stress, better navigation, foraging benefits, information transfer, and reduced predation risk (Krause & Ruxton, 2013). Over the years, many researchers have focused on understanding collective behaviour, its evolution, functional complexity and factors affecting it (Hemelrijk & Hildenbrandt, 2012; Kasumyan & Pavlov, 2018; Katz et al., 2011; Tunstrøm et al., 2013). Collective behaviour in swimming fish can manifest itself through two main modes: schooling and shoaling (Pitcher, 1983). Schooling involves a group of fish swimming together and interacting in an organized and coordinated way, while shoaling involves groups that stay close together without movement synchronization or polarization between individuals.

In the aquatic environment, hydrodynamic forces play an important role in shaping collective behaviour because they influence both the speed at which information

propagates through a group as well as the structure of the group itself (Chicoli et al., 2014; Pavlov & Kasumyan, 2000; Strandburg-Peshkin et al., 2013). For instance, high turbulence levels can disguise the presence of other fish that would usually be detected through their sensory line, thus reducing their ability to detect and transfer information to other group members, as well as stimuli response of the whole group (Chicoli et al., 2014). Additionally, hydrodynamics can affect school structure by influencing where individuals position themselves within a school due to favourable, energy-saving flow conditions (Pavlov & Kasumyan, 2000). Here, we illustrate key aspects of collective behaviour that could be relevant from the perspective of fish passage research and design.

2.1 Energy expenditure

The reduction in locomotion costs associated with schooling is confirmed in the literature by multiple experimental studies. By analysing tail beat frequency and oxygen consumption, it was observed that energy savings associated with schooling might exceed 20% in golden shiners (*Notemigonus crysoleucas*, Fish et al., 1991), sea bass (*Dicentrarchus labrax*, Herskin & Steffensen, 1998), and roach (*Rutilus rutilus*, Svendsen et al., 2003). These reduced locomotion costs were found to be related to the position of fish in the school, with trailing individuals saving more energy compared to the fish in front of the school. Additionally, Marras et al. (2015) found that grey mullet (*Liza aurata*) swimming in a group would have reduced swimming costs regardless of their position in the school. From tail beat frequency analysis, they observed that even individuals swimming in front of their neighbours would gain energetic benefits compared to fish swimming in isolation at the same speed, although less than companions swimming at the rear of the school.

Despite this experimental evidence, mechanisms for which fish save energy while schooling remain not fully understood, and the research community still does not converge on one theoretical framework. The idea that synchronized movement could bring energetic benefits due to the exploitation of hydrodynamics dates back to the theory of Weihs (1973), who proposed a 2-dimensional model of schooling fish improving swimming performances by assuming a diamond-shaped configuration. Even if a diamond pattern could justify the decreased energy costs of moving in water, no evidence of a consistent occurrence of this configuration has been observed in nature. The limitations of such theory lay in the strictly 2D approach, as well as the assumption of fish keeping a constant position relative to the group and not adapting to flow gradients.

Different studies have then proposed models coupling behavioural rules with hydrodynamics, trying to depict the complexity of interactions among individuals at different flow conditions. Gazzola et al. (2016) first proposed a model using vortex

dipoles to represent swimmers, showing that – in contrast with classical agent-based model rules - a reinforcement learning algorithm could explain the adaptive response of individual swimmers and, therefore, schooling in complex hydrodynamic environments. Verma et al. (2018) also used reinforcement learning to find positions where numerically simulated swimmers could best exploit the shed vortices created by neighbouring fish. They found that when fish place themselves following off-centre a steady leader, they could gain energy benefits by synchronizing the head movement with the wakes even in unsteady flows. Filella et al. (2018) used numerical simulations to demonstrate the advantage of cohesive schooling in a large group of swimmers emerging from an in-line configuration.

To identify the rules governing individual interactions in schools, many studies involving laboratory experiments have been conducted. Among these, the study by Katz et al. (2011) stands out. These authors studied interactions between golden shiners (*Notemigonus crysoleucas*) swimming in groups of 2, 3, 10 and 30. The analysis of trajectories showed that individual motions do not result from linearly averaging the input from each separate neighbour (as it was commonly assumed in previous research on collective behaviour), hence highlighting the complexity of group dynamics and multi-information processing. Their work led to a successive study on collective states (i.e. swarm, milling, and polarized groups) that analysed the emerging coherent patterns of fish groups (Tunström et al., 2013). Even though these studies reveal exceptional insights into collective behaviour, no information can be derived regarding response to hydrodynamics, as they were conducted in shallow aquariums with quiescent water.

In uniform flows at different mean velocities, Ashraf et al. (2016) studied pairs of red nose tetra fish (*Hemigrammus bleheri*), revealing an increase in synchronization of the caudal fin between pairs with increasing speed, possibly related to energy savings. In addition, they observed that the distance between nearest neighbours stayed constant, arguing that it was maintained by visual contact. In contrast, Li et al. (2020) showed that pairs of goldfish (*Carassius auratus*), regardless of whether their vision or lateral line sensing were impaired, synchronized their tail-beat movement depending on their front-back distance (a strategy referred to as ‘vortex phase matching’). De Bie et al. (2020) observed that the preferred configuration of pairs of Eurasian minnows (*Phoxinus phoxinus*) depended on the mean flow velocity. Fish showed a higher tendency to swim closely in a side-by-side configuration at high velocities, whereas, in the absence of flow, they tended to minimize visual impediments by employing a ‘leader-follower’ strategy. In another study by Ashraf et al. (2017), where 3D positions of red nose tetra fish were recorded at different flow velocities, it was also found that fish tended to swim side-by-side at high speeds.

Overall, these studies consistently demonstrate that schooling is very much affected by mean flow velocities in ways that seem to promote energy-saving in predominantly shallow flows where swimming is essentially constrained over two dimensions. Very

little is known about energy-saving strategies adopted by individuals swimming in three-dimensional flow domains. Moreover, the effects of other hydrodynamic metrics on schooling, such as turbulence, remain to be studied.

Principles of fish pass design aiming at recreating suitable hydrodynamic conditions are commonly based on swimming performance curves of fish swimming alone. As far as energy expenditure is concerned, this probably represents a conservative (hence effective) design approach. It is crucial to understand how individual fish in schools conserve energy while swimming in hydrodynamically complex environments in order to model their swimming behaviour and contribute to the proper design of fishways.

2.2 Navigation

Migration is often undertaken in large groups for many taxa, including fish (Couzin, 2018; Milner-Gulland et al., 2011). Experimental studies showed that fish can better follow migration routes with other conspecifics and that homing accuracy usually increases with group size (Berdahl et al., 2013, 2017; Couzin et al., 2005). Over time, different explanations for this phenomenon have been suggested.

According to the ‘*many wrongs*’ principle, groups can average out information errors individuals make, resulting in higher accuracy (Bode et al., 2012; Codling et al., 2007; Simons, 2004). The *leadership* theory, instead, considers navigation led by informed individuals that guide the rest towards the correct destination (Couzin et al., 2005). Another explanation is that information passes progressively from informed individuals to uninformed ones over time, what is called *social learning* (De Luca et al., 2014; Fagan et al., 2012; Huse et al., 2002). *Collective learning* consists instead of the generation of navigation information of the group over time through social interactions (Kao et al., 2014). Finally, *emergent sensing* consists of the ability of the group as a whole to sense and follow gradients through social interactions, like a distributed sensor (Berdahl et al., 2013).

These mechanisms are not mutually exclusive, and navigation can result from a complex interplay between them, which might depend on species, life stage, environment, and navigational task (Berdahl et al., 2018). In fact, navigation is not used exclusively for migration but also for other tasks such as finding food, shelter, or the entrance of a fish pass (Berdahl et al., 2018; Goodwin et al., 2014; Okasaki et al., 2020). As a result, collective navigation may result in an easier and faster discovery of a fish pass entrance (Berdahl et al., 2016). Additionally, individuals passing a fishway alone, separated from the rest of their group, may face problems continuing migration, particularly along a highly engineered river with multiple consecutive fish passes. Group fragmentation caused by a challenging and delayed movement through a fish pass may inhibit the ability of fish to home successfully. Despite this aspect being recognised as very relevant by the scientific community (Berdahl et al., 2017; Brown &

Laland, 2003; Okasaki et al., 2020), very little is known about the effect of fishway hydrodynamics on school fragmentation.

2.3 Stress

Since schooling provides antipredator benefits thanks to dilution and confusion effects (Lehtonen & Jaatinen, 2016; Morgan & Godin, 1985; Turner & Pitcher, 1986; Wrona & Dixon, 1991), it may reduce the need for vigilance and thereby reduce stress. In salmonid species, social hierarchies can cause social stress (Ejike & Schreck, 1980; Fernandes & Volpato, 1993; Sloman et al., 2000, 2001), but for most gregarious animals, the presence of conspecifics results in physiological benefits by significantly lowering metabolic rates. This phenomenon - commonly referred to as the 'calming effect' - has been observed in different gregarious fish (Lefrançois et al., 2009; Nadler et al., 2016; Queiroz & Magurran, 2005; Schleuter et al., 2007), regardless of whether or not they swim in schools (Parker, 1973). Moreover, social interactions can result in a faster recovery from stress, as solitary fish take longer to return to a normal physiological state after an acute stress event than fish in groups (Allen et al., 2009; Culbert et al., 2019; Queiroz & Magurran, 2005).

These insights highlight the importance of collective behaviour in fish passes from a physiological perspective. In fact, fish passes must not only facilitate the movement across a barrier but also ensure that the process does not cause excessive stress on the fish. This is because the crossing of a fish pass has the potential to cause acute stress in fish, which can temporarily impact various physiological aspects, such as metabolism (Mushtaq et al., 2014), memory (Gaikwad et al., 2011), and locomotion (Otsuka et al., 2022). From this point of view, it seems imperative to design fishway hydrodynamics to avoid as much as possible group fragmentation not only to improve navigation but also to minimise stress levels during migration. Lower stress levels in groups can also affect behaviour and potentially increase the passage performance of migrating fish (Gregory & Wood, 1999).

2.4 Exploration

The trade-off between searching for resources and avoiding predators affects the degree of exploratory behaviour of fish. Exploration is usually linked with an individual's inclination to take risks (also referred to as *boldness*) and results from an interplay between personality traits, physiological needs and external conditions (Wilson et al., 1993). "Animal personalities" can be described as consistent and stable differences in behaviour within a population that are consistent across various contexts (Wolf & Weissing, 2012). Individuals with different behavioural types or "personality traits" exhibit suites of correlated traits, which are also known as "syndromes" (Wolf & Weissing, 2012). In groups, there will be fish that tend to assume bolder or dominant

behaviour compared to other companions (Toms et al., 2010), changing pathways of information transfer among group members (Hasenjager et al., 2020). As a result, group personality composition can influence individuals' interactions with their environment and other group mates, thus affecting foraging performances, collective decision-making and predation avoidance (Jolles et al., 2017). The willingness of a fish to take the risk to explore unfamiliar or unsheltered environments will also depend on its physiological needs (e.g. foraging or reproduction) and external conditions, such as light, predation, or hydraulic stimuli (Brown et al., 2005; Chapman et al., 2010; Kareklas et al., 2016; Klefoth et al., 2012; Roy & Bhat, 2018; Tang & Fu, 2021).

Social facilitation is the mechanism that refers to an increased level of boldness in animals in the presence of other conspecifics. Different studies proved that this phenomenon occurs in some freshwater species (Galhardo et al., 2012; Magnhagen & Bunnefeld, 2009; Ward, 2012). Magnhagen & Bunnefeld (2009) observed that fish that alone were the shiest displayed the most changes in behaviour, becoming bolder when in a group, whereas fish that exhibited a bolder personality trait kept similar behaviour in the presence of conspecifics. Cote et al. (2011) also showed that fish dispersal was affected by group mean boldness score, with individuals being more likely to disperse with bold members regardless of their own personality type.

From a fish passage perspective, a fish pass represents a novel environment. For some species, social facilitation might affect the willingness of a fish to approach and enter a fish pass (Albayrak et al., 2020). A study evaluating fish guidance structures in a downstream laboratory facility found that solitary barbels (*Barbus barbuis*) tended to seek shelter in the flume and were reluctant to move, while small groups of barbels displayed higher motivation to swim (Albayrak et al., 2020).

2.5 Predation

The attraction of predators at the entrance of fish passes is a phenomenon observed at many sites across the globe. Fish shoals concentrating in these confined areas can induce intensified predation from other larger fish, birds, mammals or reptiles (Gowans et al., 2003; Petersen et al., 1994; Ruggerone, 1986; Schilt, 2007). A combination of high population densities and long resident time at the entrance of a fish pass can result in increased predation risks (Lemasson et al., 2014).

From this perspective, shoaling provides anti-predator benefits due to an interplay of lower predation probability ('dilution effect'), lower predator success ('confusion effect'), and higher vigilance of the group as a whole (Landeau & Terborgh, 1986; Lehtonen & Jaatinen, 2016; Pitcher et al., 1986). For instance, Landeau & Terborgh (1986) observed that largemouth bass (*Micropterus salmoides*) performed better in capturing solitary silvery minnows (*Hybognathus nuchalis*) than when they were in a group, taking much longer to prey as school size was increased, as a result of the

‘confusion effect’. The ‘dilution effect’ instead, indicates the lower chance for an individual to be captured when in the presence of other potential prey and has been observed in different experimental studies (Lehtonen & Jaatinen, 2016; Morgan & Godin, 1985; Wrona & Dixon, 1991). Additionally, individuals can better discern the presence of a predator by olfactory and visual cues provided by informed group mates (Kelley & Magurran, 2003; McCormick & Manassa, 2008). Fish that have perceived the presence of a predator may change their behaviour by displaying a fright response, which other group mates can observe (Pitcher et al., 1986; Smith, 1992).

Overall, the presence of predators stalling at fish pass sites is determined by the rich abundance of fish found at the entrance or the exit of such structures (Agostinho et al., 2012). However, this significant prey concentration is likely more due to low fish pass efficiency or inevitable crowding - causing fish to congregate by the fishway entrance - rather than collective behaviour itself.

3. Implications for fish passage design and future research

The concepts presented here highlight the need to take group behaviour into account in fish passage science. We suggest taking collective behaviour into account throughout different phases of river management, including evidence-based design, implementation and monitoring. Certainly, engineers in charge of designing a fish pass could benefit from research into group behaviour of freshwater species.

For instance, laboratory investigations could provide experimental-based knowledge on schooling mechanisms and preferred flow conditions by groups, providing vital information concerning fish pass attractivity. Schools could also be investigated to find velocity and turbulence thresholds at which groups are no more able to swim coordinately and transfer vital information within.

Field studies also represent a central source of information. As biotelemetric technologies such as acoustic, PIT, and radio telemetry continue to develop rapidly, researchers are increasingly able to study fish groups in their natural habitats. Moreover, the development of user-friendly and accessible artificial intelligence techniques is converting large datasets, such as geographical position data and video recordings, to effective and time-saving sources of information on fish movement and behaviour, both in field and laboratory settings (Christin et al., 2019; Lamba et al., 2019). In the past, for instance, videos had to be manually examined by a person, but now automated object detection methods such as deep learning are becoming more available (Barreiros et al., 2021; Huang et al., 2021; Lopez-Marcano et al., 2021). Thanks to all these technologies, it is now possible to comprehensively study the relationships between passage efficiency, group size and other abiotic factors, such as light, sound and hydrodynamics.

Also, installing monitoring frameworks, such as fish counters, could help to gain insight into the behaviour of fish at existing structures (Pereira et al., 2021), even from a collective behaviour standpoint. The data provided by fish counters, which typically include the number of fish that pass through, the time taken to pass, and the number of attempts, can offer valuable insights into the efficacy of fish passage over extended periods of time. With regard to modelling, collective behaviour could be incorporated into existing approaches, such as Agent-Based Models (ABMs), often utilized to simulate fish movement and behaviour at strategic locations (Goodwin et al., 2006). Increasing the prediction performance of such models would better inform engineers, biologists and practitioners involved in freshwater conservation management.

These new data sources, combined with the expertise of professionals and researchers from different disciplines, could result in new evidence-based guidelines for fish pass design with optimized geometry and hydraulic flow conditions for gregarious species.

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