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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 m^2 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 crysofeucas*, Fish et al., 1991), sea bass (*Dicentrarchus labrax*, Herskin & Steffensen, 1998), and roach (*Rutilus rutilusI*, 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 (*Notemigonous 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 (Tunstrøm 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 solitaire 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 barbus*) 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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References

Agostinho, A. A., Agostinho, C. S., Pelicice, F. M., & Marques, E. E. (2012). Fish ladders: Safe fish passage or hotspot for predation? *Neotropical Ichthyology*, *10*(4), 687–696. https://doi.org/10.1590/S1679-62252012000400001

Albayrak, I., Boes, R. M., Kriewitz-Byun, C. R., Peter, A., & Tullis, B. P. (2020). Fish guidance structures: Hydraulic performance and fish guidance efficiencies. *Journal of Ecohydraulics*, *5*(2), 113–131.

Allen, P. J., Barth, C. C., Peake, S. J., Abrahams, M. V., & Anderson, W. G. (2009). Cohesive social behaviour shortens the stress response: The effects of conspecifics on the stress response in lake sturgeon Acipenser fulvescens. *Journal of Fish Biology*, *74*(1), 90–104. https://doi.org/10.1111/j.1095-8649.2008.02112.x

Ashraf, I., Bradshaw, H., Ha, T. T., Halloy, J., Godoy-Diana, R., & Thiria, B. (2017). Simple phalanx pattern leads to energy saving in cohesive fish schooling. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(36), 9599–9604. https://doi.org/10.1073/pnas.1706503114

Ashraf, I., Godoy-Diana, R., Halloy, J., Collignon, B., & Thiria, B. (2016). Synchronization and collective swimming patterns in fish (Hemigrammus bleheri). *Journal of the Royal Society Interface*, *13*(123). https://doi.org/10.1098/rsif.2016.0734

Barreiros, M. de O., Dantas, D. de O., Silva, L. C. de O., Ribeiro, S., & Barros, A. K. (2021). Zebrafish tracking using YOLOv2 and Kalman filter. *Scientific Reports*, *11*(1), 1–14. https://doi.org/10.1038/s41598-021-81997-9

Berdahl, A., Kao, A. B., Flack, A., Westley, P. A. H., Codling, E. A., Couzin, I. D., Dell, A. I., & Biro, D. (2018). Collective animal navigation and migratory culture: From theoretical models to empirical evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746). https://doi.org/10.1098/rstb.2017.0009

Berdahl, A., Torney, C. J., Ioannou, C. C., Faria, J. J., & Couzin, I. D. (2013). Emergent sensing of complex environments by mobile animal groups. *Science*, *339*(6119), 574–576. https://doi.org/10.1126/science.1225883

Berdahl, A., Westley, P. A. H., Levin, S. A., Couzin, I. D., & Quinn, T. P. (2016). A collective navigation hypothesis for homeward migration in anadromous salmonids. *Fish and Fisheries*, *17*(2), 525–542. https://doi.org/10.1111/faf.12084

Berdahl, A., Westley, P. A. H., & Quinn, T. P. (2017). Social interactions shape the timing of spawning migrations in an anadromous fish. *Animal Behaviour*, *126*, 221–229. https://doi.org/10.1016/j.anbehav.2017.01.020

Berga, L. (2016). The Role of Hydropower in Climate Change Mitigation and Adaptation: A Review. *Engineering*, *2*(3), 313–318. https://doi.org/10.1016/J.ENG.2016.03.004

Birnie-Gauvin, K., Candee, M. M., Baktoft, H., Larsen, M. H., Koed, A., & Aarestrup, K. (2018). River connectivity reestablished: Effects and implications of six weir removals on brown trout smolt migration. *River Research and Applications*, *34*(6), 548–554. https://doi.org/10.1002/rra.3271

Bode, N. W. F., Franks, D. W., Jamie Wood, A., Piercy, J. J. B., Croft, D. P., & Codling, E. A. (2012). Distinguishing social from nonsocial navigation in moving animal groups. *American Naturalist*, *179*(5), 621–632. https://doi.org/10.1086/665005

Brown, C., & Laland, K. N. (2003). *Social learning in fishes : a review*.

Brown, G. E., Bongiorno, T., Dicapua, D. M., Ivan, L. I., & Roh, E. (2005). *Effects of group size on the threat-sensitive response to varying concentrations of chemical alarm cues by juvenile convict cichlids 1*. https://doi.org/10.1139/Z05-166

Bunt, C. M., Castro-Santos, T., & Haro, A. (2012). Performance of fish passage structures at upstream barriers to migration. *River Research and Applications*, *28*(4), 457–478. https://doi.org/10.1002/rra.1565

Castro-Santos, T. (2005). Optimal swim speeds for traversing velocity barriers: An analysis of volitional high-speed swimming behavior of migratory fishes. *Journal of Experimental Biology*, *208*(3), 421–432. https://doi.org/10.1242/jeb.01380

Castro-Santos, T., Cotel, A., & Webb, P. W. (2009). Fishway evaluations for better bioengineering: an integrative approach. *Challenges for Diadromous Fishes in a Dynamic Global Environment. American Fisheries Society, Symposium*, *69*, 557–575.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), 9–13. https://doi.org/10.1126/sciadv.1400253

Chapman, B. B., Morrell, L. J., Krause, J., Biology, C., & Fisheries, I. (2010). *Unpredictability in food supply during early life influences boldness in fish*. *February*. https://doi.org/10.1093/beheco/arq003

Chicoli, A., Butail, S., Lun, Y., Bak-Coleman, J., Coombs, S., & Paley, D. A. (2014). The effects of flow on schooling Devario aequipinnatus: School structure, startle response and information transmission. *Journal of Fish Biology*, *84*(5), 1401–1421. https://doi.org/10.1111/jfb.12365

Christin, S., Hervet, É., & Lecomte, N. (2019). Applications for deep learning in ecology. *Methods in Ecology and Evolution*, *10*(10), 1632–1644.

Clay, C. H. (1995). Design of fishways and other fish facilities. In *Design of Fishways and Other Fish Facilities*. CRC Press. https://doi.org/10.1201/9781315141046

Codling, E. A., Pitchford, J. W., & Simpson, S. D. (2007). Group navigation and the "many-wrongs principle" in models of animal movement. *Ecology*, *88*(7), 1864–1870. https://doi.org/10.1890/06-0854.1

Cote, J., Fogarty, S., Brodin, T., Weinersmith, K., & Sih, A. (2011). Personality-dependent dispersal in the invasive mosquitofish: Group composition matters. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1712), 1670–1678. https://doi.org/10.1098/rspb.2010.1892

Couzin, I. D. (2018). Collective animal migration. *Current Biology*, *28*(17), R976–R980. https://doi.org/10.1016/j.cub.2018.04.044

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*(7025), 513–516.

Culbert, B. M., Gilmour, K. M., & Balshine, S. (2019). Social buffering of stress in a group-living fish. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1910), 20191626. https://doi.org/10.1098/rspb.2019.1626

De Bie, J., Manes, C., & Kemp, P. S. (2020). Collective behaviour of fish in the presence and absence of flow. *Animal Behaviour*, *167*, 151–159. https://doi.org/10.1016/j.anbehav.2020.07.003

De Luca, G., Mariani, P., MacKenzie, B. R., & Marsili, M. (2014). Fishing out collective memory of migratory schools. *Journal of the Royal Society Interface*, *11*(95), 20140043.

Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W. M., Marconi, V., McRae, L., Baumgartner, L. J., Brink, K., Claussen, J. E., Cooke, S. J., Darwall, W., Eriksson Britas Klemens, De Leaniz, C. G., Hogan, Z., Royte, J., Silva, L. G. M., Thieme, M., Tickner, D., Waldman, J., … Berkhuysen, A. (2020). *The Living Planet Index (LPI) for migratory freshwater fish*. 55 pp. https://worldfishmigrationfoundation.com/living-planet-index-2020

Dixit, A. (2003). Floods and vulnerability: Need to rethink flood management. *Natural Hazards*, *28*(1), 155–179. https://doi.org/10.1023/A:1021134218121

Ead, S. A., Katopodis, C., Sikora, G. J., & Rajaratnam, N. (2004). Flow regimes and structure in pool and weir fishways. *Journal of Environmental Engineering and Science*, *3*(5), 379–390. https://doi.org/10.1139/S03-073

Edenhofer, O., Pichs-Madruga, R., Sokona, Y., Seyboth, K., Kadner, S., Zwickel, T., Eickemeier, P., Hansen, G., Schlömer, S., & Von Stechow, C. (2011). *Renewable energy sources and climate change mitigation: Special report of the intergovernmental panel on climate change*. Cambridge University Press.

Ejike, C., & Schreck, C. B. (1980). Stress and Social Hierarchy Rank in Coho Salmon. *Transactions of the American Fisheries Society*, *109*(4), 423–426. https://doi.org/10.1577/1548-8659(1980)109<423:sashri>2.0.co;2

Fagan, W. F., Cantrell, R. S., Cosner, C., Mueller, T., & Noble, A. E. (2012). Leadership, social learning, and the maintenance (or collapse) of migratory populations. *Theoretical Ecology*, *5*(2), 253–264.

Fernandes, M. de O., & Volpato, G. L. (1993). Heterogeneous growth in the Nile tilapia: Social stress and carbohydrate metabolism. *Physiology and Behavior*, *54*(2), 319–323. https://doi.org/10.1016/0031-9384(93)90117-X

Filella, A., Nadal, F., Sire, C., Kanso, E., & Eloy, C. (2018). Model of Collective Fish Behavior with Hydrodynamic Interactions. *Physical Review Letters*, *120*(19), 35–37. https://doi.org/10.1103/PhysRevLett.120.198101

Fish, F. E., Fegely, J. F., & Xanthopoulos, C. J. (1991). *Burst-Anc-Coast Swimming in Schooling Fish (NOTEMIGONUS CR YSOLEUCAS) with Implications for Energy Economy*.

Gaikwad, S., Stewart, A., Hart, P., Wong, K., Piet, V., Cachat, J., & Kalueff, A. V. (2011). Acute stress disrupts performance of zebrafish in the cued and spatial memory tests: The utility of fish models to study stress–memory interplay. *Behavioural Processes*, *87*(2), 224–230.

Galhardo, L., Vitorino, A., & Oliveira, R. F. (2012). Social familiarity modulates personality trait in a cichlid fish. *Biology Letters*, *8*(6), 936–938. https://doi.org/10.1098/rsbl.2012.0500

Gazzola, M., Tchieu, A. A., Alexeev, D., De Brauer, A., & Koumoutsakos, P. (2016). Learning to school in the presence of hydrodynamic interactions. *Journal of Fluid Mechanics*, *789*, 726–749.

Goodwin, R. A., Nestler, J. M., Anderson, J. J., Weber, L. J., & Loucks, D. P. (2006). Forecasting 3-D fish movement behavior using a Eulerian–Lagrangian–agent method (ELAM). *Ecological Modelling*, *192*(1–2), 197–223.

Goodwin, R. A., Politano, M., Garvin, J. W., Nestler, J. M., Hay, D., Anderson, J. J., Weber, L. J., Dimperio, E., Smith, D. L., & Timko, M. (2014). Fish navigation of large dams emerges from their modulation of flow field experience. *Proceedings of the National Academy of Sciences*, *111*(14), 5277–5282.

Gough, P., Fernández Garrido, P., & Van Herk, J. (2018). Dam Removal: A viable solution for the future of our European rivers. *Dam Remov. Eur*.

Gowans, A. R. D., Armstrong, J. D., Priede, I. G., & Mckelvey, S. (2003). Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland. *Ecology of Freshwater Fish*, *12*(3), 177–189. https://doi.org/10.1034/j.1600-0633.2003.00018.x

Gregory, T. R., & Wood, C. M. (1999). The effects of chronic plasma cortisol elevation on the feeding behaviour, growth, competitive ability, and swimming performance of juvenile rainbow trout. *Physiological and Biochemical Zoology*, *72*(3), 286–295.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M. E., Meng, J., Mulligan, M., … Zarfl, C. (2019). Mapping the world's free-flowing rivers. *Nature*, *569*(7755), 215–221. https://doi.org/10.1038/s41586-019-1111-9

Hasenjager, M. J., Hoppitt, W., & Dugatkin, L. A. (2020). Personality composition determines social learning pathways within shoaling fish: Group personality and social learning. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1936). https://doi.org/10.1098/rspb.2020.1871

Hemelrijk, C. K., & Hildenbrandt, H. (2012). Schools of fish and flocks of birds: Their shape and internal structure by self-organization. *Interface Focus*, *2*(6), 726–737. https://doi.org/10.1098/rsfs.2012.0025

Herskin, J., & Steffensen, J. F. (1998). Energy savings in sea bass swimming in a school: measurements of tail beat frequency and oxygen consumption at different swimming speeds. *Journal of Fish Biology*, *53*(2), 366–376.

Huang, Z. J., He, X. X., Wang, F. J., & Shen, Q. (2021). A Real-Time Multi-Stage Architecture for Pose Estimation of Zebrafish Head with Convolutional Neural Networks. *Journal of Computer Science and Technology*, *36*(2), 434–444. https://doi.org/10.1007/s11390-021-9599-5

Huse, G., Railsback, S., & Feronö, A. (2002). Modelling changes in migration pattern of herring: collective behaviour and numerical domination. *Journal of Fish Biology*, *60*(3), 571–582.

Jolles, J. W., Boogert, N. J., Sridhar, V. H., Couzin, I. D., & Manica, A. (2017). Consistent Individual Differences Drive Collective Behavior and Group Functioning of Schooling Fish. *Current Biology*, *27*(18), 2862-2868.e7. https://doi.org/10.1016/j.cub.2017.08.004

Kao, A. B., Miller, N., Torney, C., Hartnett, A., & Couzin, I. D. (2014). Collective learning and optimal consensus decisions in social animal groups. *PLoS Computational Biology*, *10*(8), e1003762.

Kareklas, K., Arnott, G., Elwood, R. W., & Holland, R. A. (2016). Plasticity varies with boldness in a weakly-electric fish. *Frontiers in Zoology*, 1–7. https://doi.org/10.1186/s12983-016-0154-0

Kasumyan, A. O., & Pavlov, D. S. (2018). Evolution of schooling behavior in fish. *Journal of Ichthyology*, *58*(5), 670–678. https://doi.org/10.1134/S0032945218050090

Katopodis, C., Kells, J. A., & Acharya, M. (2001). Nature-like and conventional fishways: Alternative concepts? *Canadian Water Resources Journal*, *26*(2), 211–232. https://doi.org/10.4296/cwrj2602211

Katopodis, C., & Williams, J. G. (2012). The development of fish passage research in a historical context. *Ecological Engineering*, *48*, 8–18. https://doi.org/10.1016/j.ecoleng.2011.07.004

Katz, Y., Tunstrøm, K., Ioannou, C. C., Huepe, C., & Couzin, I. D. (2011). Inferring the structure and dynamics of interactions in schooling fish. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(46), 18720–18725. https://doi.org/10.1073/pnas.1107583108

Kelley, J. L., & Magurran, A. E. (2003). Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, *4*(3), 216–226.

Klefoth, T., Skov, C., Krause, J., & Arlinghaus, R. (2012). *The role of ecological context and predation risk-stimuli in revealing the true picture about the genetic basis of boldness evolution in fish*. 547–559. https://doi.org/10.1007/s00265-011-1303-2

Krause, J., & Ruxton, G. D. (2013). Living in Groups. In *Transactional Analysis Journal* (Vol. 43, Issue 4). Oxford University Press. https://doi.org/10.1177/0362153713519414

Lamba, A., Cassey, P., Segaran, R. R., & Koh, L. P. (2019). Deep learning for environmental conservation. *Current Biology*, *29*(19), R977–R982.

Landeau, L., & Terborgh, J. (1986). Oddity and the 'confusion effect'in predation. *Animal Behaviour*, *34*(5), 1372–1380.

Larinier, M. (2002). Pool Fishways, Pre-Barrages and Natural Bypass Channels. *Bulletin Français de La Pêche et de La Pisciculture*, *364*(364 supplément), 54–82. https://doi.org/10.1051/kmae/2002108

Lefrançois, C., Ferrari, R. S., Moreira Da Silva, J., & Domenici, P. (2009). The effect of progressive hypoxia on spontaneous activity in single and shoaling golden grey mullet Liza aurata. *Journal of Fish Biology*, *75*(7), 1615–1625. https://doi.org/10.1111/j.1095-8649.2009.02387.x

Lehner, B., Liermann, C. R., Revenga, C., Vörömsmarty, C., Fekete, B., Crouzet, P., Döll, P., Endejan, M., Frenken, K., Magome, J., Nilsson, C., Robertson, J. C., Rödel, R., Sindorf, N., & Wisser, D. (2011). High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. *Frontiers in Ecology and the Environment*, *9*(9), 494–502. https://doi.org/10.1890/100125

Lehtonen, J., & Jaatinen, K. (2016). Safety in numbers: the dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology*, *70*(4), 449–458. https://doi.org/10.1007/s00265-016-2075-5

Lemasson, B. H., Haefner, J. W., & Bowen, M. D. (2014). Schooling increases risk exposure for fish navigating past artificial barriers. *PLoS ONE*, *9*(9). https://doi.org/10.1371/journal.pone.0108220

Li, L., Nagy, M., Graving, J. M., Bak-Coleman, J., Xie, G., & Couzin, I. D. (2020). Vortex phase matching as a strategy for schooling in robots and in fish. *Nature Communications*, *11*(1), 1–9. https://doi.org/10.1038/s41467-020-19086-0

Lopez-Marcano, S., L. Jinks, E., Buelow, C. A., Brown, C., Wang, D., Kusy, B., M. Ditria, E., & Connolly, R. M. (2021). Automatic detection of fish and tracking of movement for ecology. *Ecology and Evolution*, *11*(12), 8254–8263. https://doi.org/10.1002/ece3.7656

López-Moreno, J. I., Vicente-Serrano, S. M., Beguería, S., García-Ruiz, J. M., Portela, M. M., & Almeida, A. B. (2009). Dam effects on droughts magnitude and duration in a transboundary basin: The Lower River Tagus, Spain and Portugal. *Water Resources Research*, *45*(2).

Magnhagen, C., & Bunnefeld, N. (2009). Express your personality or go along with the group: What determines the behaviour of shoaling perch? *Proceedings of the Royal Society B: Biological Sciences*, *276*(1671), 3369–3375. https://doi.org/10.1098/rspb.2009.0851

Marras, S., Killen, S. S., Lindström, J., McKenzie, D. J., Steffensen, J. F., & Domenici, P. (2015). Fish swimming in schools save energy regardless of their spatial position. *Behavioral Ecology and Sociobiology*, *69*(2), 19–226. https://doi.org/10.1007/s00265-014-1834-4

Mccormick, M. I., & Manassa, R. (2008). Predation risk assessment by olfactory and visual cues in a coral reef fish. *Coral Reefs*, *27*(1), 105–113.

Milner-Gulland, E. J., Fryxell, J. M., & Sinclair, A. R. E. (2011). *Animal migration: a synthesis*. OUP Oxford.

Morgan, M. J., & Godin, J. J. (1985). Antipredator benefits of schooling behaviour in a cyprinodontid fish, the banded killifish (Fundulus diaphanus). *Zeitschrift Für Tierpsychologie*, *70*(3), 236–246.

Mushtaq, M. Y., Marçal, R. M., Champagne, D. L., Van Der Kooy, F., Verpoorte, R., & Choi, Y. H. (2014). Effect of acute stresses on zebra fish (Danio rerio) metabolome measured by NMR-based metabolomics. *Planta Medica*, *80*(14), 1227–1233.

Nadler, L. E., Killen, S. S., McClure, E. C., Munday, P. L., & McCormick, M. I. (2016). Shoaling reduces metabolic rate in a gregarious coral reef fish species. *Journal of Experimental Biology*, *219*(18), 2802–2805.

Noonan, M. J., Grant, J. W. A., & Jackson, C. D. (2012a). *A quantitative assessment of fish passage efficiency*. 450–464. https://doi.org/10.1111/j.1467-2979.2011.00445.x

Noonan, M. J., Grant, J. W. A., & Jackson, C. D. (2012b). A quantitative assessment of fish passage efficiency. *Fish and Fisheries*, *13*(4), 450–464.

Northcote, T. G. (1978). Migratory strategies and production in freshwater fishes. *Ecology of Freshwater Fish Production*, 326–359.

Odeh, M. (1999). Fish passage innovation for ecosystem and fishery restoration. *American Fisheries Society*, 24.

Okasaki, C., Keefer, M. L., Westley, P. A. H., & Berdahl, A. (2020). Collective navigation can facilitate passage through human-made barriers by homeward migrating Pacific salmon: Collective navigation improves passage. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1937). https://doi.org/10.1098/rspb.2020.2137rspb20202137

Otsuka, A., Shimomura, Y., Sakikubo, H., Miura, K., & Kagawa, N. (2022). Effects of single and repeated heat stress on anxiety-like behavior and locomotor activity in medaka fish. *Fisheries Science*, 1–10.

Parker, F. R. (1973). Reduced Metabolic Rates in Fishes as a Result of Induced Schooling. *Transactions of the American Fisheries Society*, *102*(1), 125–131. https://doi.org/10.1577/1548-8659(1973)102<125:rmrifa>2.0.co;2

Pavlov, D. S., & Kasumyan, A. O. (2000). Patterns and mechanisms of schooling behaviour in fish: A review. *Journal of Ichthyology*, *40*(2), 163–231.

Pereira, E., Quintella, B. R., Lança, M. J., Alexandre, C. M., Mateus, C. S., Pedro, S., Belo, A. F., Rato, A. S., Quadrado, M. F., Telhado, A., Batista, C., & Almeida, P. R. (2021). Temporal patterns of the catadromous thinlip grey mullet migration in freshwater. *Ecohydrology*, *14*(8), e2345.

https://doi.org/10.1002/eco.2345

Petersen, J. H., Gadomski, D. M., & Poe, T. P. (1994). Differential predation by northern squawfish (Ptychocheilus oregonensis) on live and dead juvenile salmonids in the Bonneville Dam Tailrace (Columbia River). *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(5), 1197–1204. https://doi.org/10.1139/f94-119

Pitcher, T. J. (1983). Heuristic definitions of fish shoaling behaviour. *Animal Behaviour*, *31*(2), 611–613. https://doi.org/10.1016/S0003-3472(83)80087-6

Pitcher, T. J., Green, D. A., & Magurran, A. E. (1986). Dicing with death: predator inspection behaviour in minnow shoals. *Journal of Fish Biology*, *28*(4), 439–448.

Quaranta, E., Katopodis, C., & Comoglio, C. (2019). Effects of bed slope on the flow field of vertical slot fishways. *River Research and Applications*, *35*(6), 656–668. https://doi.org/10.1002/rra.3428

Queiroz, H., & Magurran, A. E. (2005). Safety in numbers? Shoaling behaviour of the Amazonian red-bellied piranha. *Biology Letters*, *1*(2), 155–157.

Roscoe, D. W., & Hinch, S. G. (2010). Effectiveness monitoring of fish passage facilities: Historical trends, geographic patterns and future directions. *Fish and Fisheries*, *11*(1), 12–33. https://doi.org/10.1111/j.1467-2979.2009.00333.x

Roy, T., & Bhat, A. (2018). Repeatability in boldness and aggression among wild zebrafish (Danio rerio) from two differing predation and flow regimes. *Journal of Comparative Psychology*, *132*(4), 349.

Ruggerone, G. T. (1986). Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. *Transactions of the American Fisheries Society*, *115*(5), 736–742.

Schilt, C. R. (2007). Developing fish passage and protection at hydropower dams. *Applied Animal Behaviour Science*, *104*(3–4), 295–325. https://doi.org/10.1016/j.applanim.2006.09.004

Schleuter, D., Haertel-Borer, S., Fischer, P., & Eckmann, R. (2007). Respiration rates of Eurasian perch Perca fluviatilis and ruffe: lower energy costs in groups. *Transactions of the American Fisheries Society*, *136*(1), 43–55.

Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., Aarestrup, K., Pompeu, P. S., O'Brien, G. C., & Braun, D. C. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, *19*(2), 340–362.

Simons, A. M. (2004). Many wrongs: The advantage of group navigation. *Trends in Ecology and Evolution*, *19*(9), 453–455. https://doi.org/10.1016/j.tree.2004.07.001

Sloman, K. A., Metcalfe, N. B., Taylor, A. C., & Gilmour, K. M. (2001). Plasma cortisol concentrations before and after social stress in rainbow trout and brown trout. *Physiological and Biochemical Zoology*, *74*(3), 383–389. https://doi.org/10.1086/320426

Sloman, K. A., Motherwell, G., O'connor, K. I., & Taylor, A. C. (2000). The effect of social stress on the Standard Metabolic Rate (SMR) of brown trout, Salmo trutta. *Fish Physiology and Biochemistry*, *23*(1), 49–53. https://doi.org/10.1023/A:1007855100185

Smith, R. J. F. (1992). Alarm signals in fishes. *Reviews in Fish Biology and Fisheries*, *2*(1), 33–63.

Strandburg-Peshkin, A., Twomey, C. R., Bode, N. W. F., Kao, A. B., Katz, Y., Ioannou, C. C., Rosenthal, S. B., Torney, C. J., Wu, H. S., & Levin, S. A. (2013). Visual sensory networks and effective information transfer in animal groups. *Current Biology*, *23*(17), R709–R711.

Strayer, D. L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: Recent progress and future challenges. *Journal of the North American Benthological Society*, *29*(1), 344–358. https://doi.org/10.1899/08-171.1

Svendsen, J. C., Skov, J., Bildsoe, M., & Steffensen, J. F. (2003). Intra-school positional preference and reduced tail beat frequency in trailing positions in schooling roach under experimental conditions. *Journal of Fish Biology*, *62*(4), 834–846.

Tang, Z., & Fu, S. J. (2021). Effects of habitat conditions on the boldness and sociability of wild-caught fish (Zacco platypus) along a river. *Journal of Ethology*, *39*(3), 379–391. https://doi.org/10.1007/s10164-021-00715-0

Toms, C. N., Echevarria, D. J., & Jouandot, D. J. (2010). A Methodological Review of Personality-Related Studies in Fish: Focus on the Shy-Bold Axis of Behavior. *International Journal of Comparative Psychology*, *23*(1). https://doi.org/10.46867/ijcp.2010.23.01.08

Tunstrøm, K., Katz, Y., Ioannou, C. C., Huepe, C., Lutz, M. J., & Couzin, I. D. (2013). Collective States, Multistability and Transitional Behavior in Schooling Fish. *PLoS Computational Biology*, *9*(2). https://doi.org/10.1371/journal.pcbi.1002915

Turner, G. F., & Pitcher, T. J. (1986). Attack abatement: a model for group protection by combined avoidance and dilution. *The American Naturalist*, *128*(2), 228–240.

Verma, S., Novati, G., & Koumoutsakos, P. (2018). Efficient collective swimming by harnessing vortices through deep reinforcement learning. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(23), 5849–5854. https://doi.org/10.1073/pnas.1800923115

Ward, A. J. W. (2012). Social facilitation of exploration in mosquitofish (Gambusia holbrooki). *Behavioral Ecology and Sociobiology*, *66*(2), 223–230. https://doi.org/10.1007/s00265-011-1270-7

Watson, J. M., Coghlan, S. M., Zydlewski, J., Hayes, D. B., & Kiraly, I. A. (2018). Dam Removal and Fish Passage Improvement Influence Fish Assemblages in the Penobscot River, Maine. *Transactions of the American Fisheries Society*, *147*(3), 525–540. https://doi.org/10.1002/tafs.10053

Weihs, D. (1973). Hydromechanics of fish schooling. *Nature*, *241*(5387), 290–291.

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (Lepomis gibbosus): an ecological study of a psychological trait. *Journal of Comparative Psychology*, *107*(3), 250–260. https://doi.org/10.1037/0735-7036.107.3.250

Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, *27*(8), 452–461.

Wrona, F. J., & Dixon, R. W. J. (1991). Group size and predation risk: a field analysis of encounter and dilution effects. *The American Naturalist*, *137*(2), 186–201.

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences*, *77*, 161–170.