

Causes and Consequences of Cognitive Variation in Fishes

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Fishes are not only the largest, but also the most diverse group of vertebrates. Fishes inhabit a wide range of habitats and exhibit remarkable diversity in life history, morphology, physiology, behaviour, and ecology [1]. Differences in life history, ecology, and social systems have likely shaped cognition in fishes, but our understanding of fish cognition is still limited relative to that of other taxa [2]. Understanding how and why cognition varies within and between species will ultimately help us to understand the selective pressures shaping cognitive phenotypes in fishes and how they have adapted to their environments. This Special Issue—a collection of the most recent articles from experts in the field of fish cognition—aims to further our understanding of the evolutionary drivers of cognitive variation in fishes. Fish cognition is a rapidly developing research area [3,4], and with this Special Issue, we wish to particularly highlight four considerations for future studies of fish cognition.

First, more studies investigating the causes and consequences of individual variation in fish cognition are needed. Studies investigating the drivers of cognitive evolution have traditionally taken a comparative approach, typically contrasting measures of neuroanatomy across multiple species [5]. More recently, an increasing number of studies are taking an intraspecific approach to the study of cognition, focusing on the causes and consequences of individual variation in cognition [6]. In this vein, recent studies have found relationships between individual cognitive performance and the social environment (e.g., group size [7,8] and social network position [9]), the physical environment (e.g., elevation [10]), and predation pressure [11]. Such findings, coupled with studies linking individual variation in cognition to measures of fitness, have the potential to reveal profound insights into cognitive evolution and further our understanding of selection acting on cognitive phenotypes. Whilst an increasing number of studies are investigating the causes of individual variation in cognition, comparatively few have looked at the consequences of cognitive variation [5], and of those that do exist, there is a considerable taxonomic bias. A recent meta-analysis [12] identified 91 studies that have investigated the relationship between cognition and fitness, and of these, 21 studies investigated the relationship in fishes. While this is a reasonable proportion, within these 21 studies, only 7 species have been studied, with one species (guppy, *Poecilia reticulata*) making up >60% of studies. In order to truly understand the factors governing cognitive variation, such taxonomic biases need to be addressed, both across and within classes. Furthermore, the majority of studies investigating the relationship between cognition and fitness were carried out in captivity (58%, [12]). This pattern translates to 53% of studies across all non-fish taxa, but up to 76% within fishes [12]. Such a pattern is understandable, particularly within fishes, as the logistical challenges associated with quantifying cognitive performance in the wild, and



Citation: Braga Goncalves, I.; Ashton, B.J.; Fischer, S. Causes and Consequences of Cognitive Variation in Fishes. *Fishes* **2023**, *8*, 277. <https://doi.org/10.3390/fishes8060277>

Received: 12 May 2023

Accepted: 16 May 2023

Published: 24 May 2023



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subsequently tracking reproductive success, are substantial. However, it cannot be overlooked that studies examining the relationship between reproductive success and cognition in the wild are more ecologically relevant than laboratory-based studies. It is therefore imperative that tractable study systems, where cognitive testing in the wild is possible, are identified and/or utilised to advance our understanding of the selection pressures driving cognitive phenotypes in fishes.

Second, we believe that the use of mesocosm setups will increase the ecological validity of fish cognition studies where conducting studies in the field would be unfeasible. Mesocosms—enclosed or semi-enclosed controlled outdoor experimental units that simulate aquatic environments—are widely used in marine and freshwater ecology to study ecosystem responses to, for instance, changes in nutrient or light availability [13,14]. Such setups allow researchers to bridge the gap in ecological realism that exists between laboratory and wild environments by exposing organisms to natural variations in light and temperature, potential aerial predators, and more complex social and physical environments while retaining the ability to monitor subjects for prolonged periods of time [15]. Although less common, mesocosm studies have also been used successfully to study fish behaviour [16,17]. Ongoing advances in video tracking and in automated operant conditioning systems for fish [18–20] continue to expand the scope of studies that can be performed as well as the breadth of taxa that can be studied. Moreover, outdoor facilities available at many marine research stations (e.g., see the Association of European Marine Biological Laboratories Expanded (ASSEMBLE⁺)) can provide ideal infrastructure for mesocosm cognition studies that many universities likely lack. Incidentally, the distribution of such facilities worldwide should further promote the study of a wider range of species with varying life histories, social systems, and ecologies.

Third, more studies are needed to test whether general intelligence (g) exists in fishes. This is important to better understand the evolution of cognition in general and to resolve the long-standing debate about whether cognition is organised in a domain-specific or domain-general way (e.g., [20,21]). We are aware of only one study conducting a series of cognitive tests to assess the presence of g in an ectothermic vertebrate [22]. This study compared the performance of wild-caught cleaner wrasses (*Labroides dimidiatus*) in four cognitive tasks that have also been used to assess g in mammals. The study did not find significant correlations between the performance of cleaner wrasses between the tasks and concluded that there is no evidence of g in fishes—this is in stark contrast to endotherms such as mammals. Conversely, La Loggia and colleagues [23] found that *Neolamprologus pulcher*, a highly social cichlid from Lake Tanganyika, uses transitive inference (TI), which is the ability to infer relationships between stimuli, in a non-social context. Although the authors only used one cognitive task in this study, the result might show evidence for g in this fish species because other social cichlids from Lake Tanganyika use TI in social contexts [24,25] and *N. pulcher* are able to track the relative rank of other group members [26]. Along the same line, Reyes-Contreras et al. [27] found that an early-life cortisol treatment reduced non-social flexibility in *N. pulcher* later in life. This result is in line with other studies showing that an early-life cortisol treatment reduces social flexibility in the same species [28]. Collectively, the studies using *N. pulcher* could be used as evidence for g in a fish species. Nevertheless, confirmatory work that assesses cognitive performance in the same individuals across different cognitive domains is needed. Cichlids from Lake Tanganyika are an ideal study system to further investigate g in fishes because many closely related species that differ in their ecology and sociality can be studied in the same habitat.

Fourth, fishes are also ideal to probe the validity of classic cognitive tasks that are used to test higher cognitive abilities in other species. This is important if we seek to better understand the evolution of cognitive abilities and intelligence in general. For example, in a series of experiments, Kohda and colleagues [29–31] conclusively confirmed that cleaner wrasses pass the “mirror test”. This classic test paradigm was designed to show self-recognition in animals by applying colour dots to body parts that are not visible to the individual. It is thought that the individual has a form of self-recognition if it starts

to investigate the body part with the colour dot in front of a mirror. This assumed high level of cognition has thus far been attributed only to a handful of species (chimpanzees, *Pan troglodytes*; bottlenose dolphins, *Tursiops truncatus*; Asian elephants, *Elephas maximus*; and Eurasian magpies, *Pica pica*; see [32]). The species passing this test are considered cognitively advanced because they also have a particularly large brain relative to their body size. The controversial studies using cleaner wrasses challenge this simplistic view and show that even a species without a particularly enlarged brain relative to body size [33] can pass the mirror test. It is open for debate whether this shows that cleaner wrasses are also cognitively advanced, or that self-recognition does not require superior cognitive abilities, but this issue has further highlighted the importance of testing classic cognitive test paradigms in fishes. Investigation of the neuronal mechanisms that underlie cognitive abilities in fishes and other taxa should help to clarify whether similar brain areas are activated during engagement with the same cognitive task.

In summary, studying the causes and consequences of individual variation in fish cognition has the potential to provide novel insights into the evolution of animal cognition. Our list of future research priorities related to fish cognition is not exhaustive, but we hope to inspire and encourage researchers to study these highly promising research questions. In the following Special Issue, we collected articles within but also outside these four considerations to highlight the breadth of research on fish cognition.

Author Contributions: Conceptualization, I.B.G., B.J.A. and S.F.; writing—original draft preparation, I.B.G., B.J.A. and S.F.; writing—review and editing, I.B.G., B.J.A. and S.F. All authors have read and agreed to the published version of the manuscript.

Funding: S.F. is supported by the Vienna Science and Technology Fund (awarded to Sabine Tebbich, CS18-042). B.J.A. is supported by an Australian Research Council Discovery Early Career Researcher Award (DE220100096).

Conflicts of Interest: The authors declare no conflict of interest.

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