



Understanding fish cognition: a review and appraisal of current practices

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Abstract

With over 30,000 recognized species, fishes exhibit an extraordinary variety of morphological, behavioural, and life-history traits. The field of fish cognition has grown markedly with numerous studies on fish spatial navigation, numeracy, learning, decision-making, and even theory of mind. However, most cognitive research on fishes takes place in a highly controlled laboratory environment and it can therefore be difficult to determine whether findings generalize to the ecology of wild fishes. Here, we summarize four prominent research areas in fish cognition, highlighting some of the recent advances and key findings. Next, we survey the literature, targeting these four areas, and quantify the nearly ubiquitous use of captive-bred individuals and a heavy reliance on lab-based research. We then discuss common practices that occur prior to experimentation and within experiments that could hinder our ability to make more general conclusions about fish cognition, and suggest possible solutions. By complementing ecologically relevant laboratory-based studies with in situ cognitive tests, we will gain further inroads toward unraveling how fishes learn and make decisions about food, mates, and territories.

Keywords Teleosts · Memory · Intelligence · Learning · Behavior · Decision-making

Introduction

Over the last few decades, interest in the fields of animal cognition and cognitive ecology has increased dramatically (Brown et al. 2011; Bshary and Brown 2014; Dukas 1998; Dukas and Ratcliffe 2009). Studies of animal cognition aim to understand the processes that help animals make decisions (e.g., perception, learning, and memory; Ebbesson and Braithwaite 2012). Fishes are well suited for such cognitive studies and have become regular experimental subjects in

cognitive research. The more than 30,000 species of fishes provide valuable subjects for cognitive studies because of their taxonomic diversity, variety of habitats, and range of life-history strategies (Patton and Braithwaite 2015). Despite the growing interest in the cognitive ecology of fishes, studies to date have focused on standard laboratory models, and only a handful of fish cognition experiments have been conducted in the field or on wild fish. Captivity can have severe impacts on cognition both due to plasticity during an individual's lifetime and via artificial selection over multiple generations in the laboratory. Thus, the reliance on captive-bred fishes may limit our understanding of fish cognition in nature. Noting this strong laboratory bias and the accompanying gap in our knowledge, we embarked on this systematic survey and commentary of fish cognition research. Our objective is to bring attention to the biases present in the literature and to encourage the thoughtful design of ecologically relevant experiments. Before discussing the findings of our literature survey, we first provide a brief synopsis describing our current understanding of fish cognition.

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What we know about fish cognition

The field of fish cognition has a reasonably long history, as comparative psychologists studied goldfish (*Carassius auratus*) alongside rats and pigeons for over 100 years (Churchill Jr 1916). In the last decade, several excellent review papers have been published on the topic of fish cognition (see Brown 2015; Bshary et al. 2014; Patton and Braithwaite 2015; Pouca and Brown 2018; Sneddon and Brown 2020). The research has mainly focused on four areas: (1) simple learning, (2) numeracy, (3) spatial cognition, and (4) social cognition of fishes. For the purpose of this paper, we also focus on these four areas of fish cognition, summarizing current research in each area and then organizing our survey such that our literature search targeted the practices in each area.

i. Simple learning

Learning describes an animal's ability to use information from past experiences to inform future behavior (Cauchoix and Chainé 2016). Simple learning includes non-associative forms of learning, such as habituation and sensitization. It also includes associative forms of learning, in which connections are made either between unconditioned and conditioned stimuli (classical conditioning) or between stimuli and a certain behavior (operant conditioning).

In fishes, simple learning can be rapid and long-lasting (Brown et al. 2011). For example, goldfish learned to avoid an area of a tank after a single electric shock (Riege and Cherkin 1971). Similarly, zebrafish (*Danio rerio*) learned which colors predicted electric shocks with 89% accuracy after only 2 h of training (or 20 trials; Aoki et al. 2015). Crimson spotted rainbowfish (*Melanotaenia duboulayi*) greatly improved their escape response to a novel trawl apparatus over 5 trials and they highlight the longevity that such associations can be retained, remembering learned escape-techniques for up to 11 months (Brown 2001). For many fishes, simple learning also begins early in life. Zebrafish, for example, can learn basic classical and operant conditioning tasks from as early as 4 weeks of age (Valente et al. 2012). Simple learning in fishes is pertinent to survival-related tasks like predator avoidance and foraging (Kieffer and Colgan 1992).

ii. Numerical cognition

Numerical cognition refers to the ability to discriminate between two different discrete or continuous quantities (Agrillo et al. 2011). The ability to discern quantities is widespread among vertebrates and some invertebrates, while abstract numerical representation (counting) is considered a more demanding cognitive

process and has only seldom been demonstrated in fishes (Agrillo et al. 2009; Davis and Memmott 1982). Many fishes use quantity assessment to inform ecologically important behavioural decisions (e.g., what shoal to join, where to forage, or what mating tactic to use; reviewed by Agrillo et al. 2017). For example, fishes often choose to affiliate with larger groups when given a choice between two different shoal sizes and there are numerous fitness benefits for doing so, such as improved foraging and predator defense, increased vigilance, predator confusion, and dilution of risk (Agrillo et al. 2017). However, assessing the extent of more complex numerical abilities, such as counting, requires complex experimental protocols. In mosquitofish (*Gambusia holbrooki*), individuals showed a preference for larger shoals even when a series of baffles meant that only one conspecific could be viewed at any given time; thus, the focal 'choosing' fish needed to count how many individuals were at each end of the arena (Dadda et al. 2009). It seems that true numerical representation by fishes is largely limited to numbers no greater than 4 or 5, while ratios are typically used to compare larger quantities, consistent with many mammalian studies (Agrillo et al. 2017). For instance, mosquitofish discriminated between two shoals that differed in number by a single individual when each shoal had fewer than 5 fish, but discrimination between larger shoals was only possible if the bigger of the two had twice as many individuals or more (Agrillo et al. 2008).

iii. Spatial cognition

Spatial cognition is the ability to acquire and reorganize spatial information to make sense of an environment (Poucet 1993). Spatial cognition plays a role in many behavioural processes including foraging, mating, predator avoidance, and migration (Fukumori et al. 2010). Animals can navigate space using orientation (egocentric) or mapping (allocentric) strategies and some fishes, such as goldfish, rely on both (Rodríguez et al. 1994). Other species, like the weakly electric elephantnose fish *Gnathonemus petersii*, preferentially use egocentric cues during maze learning experiments (Schumacher et al. 2017). In contrast, intertidal gobies (*Bathygobius soporator*) create cognitive maps of the shoreline (thereby relying primarily on allocentric cues) and use these maps to jump between nearby tide pools when threatened and then can return to their home pool quickly (Aronson 1951; Jorge et al. 2012; White and Brown 2013). To construct and use a cognitive map (i.e., a mental representation of an environment), an animal needs to: (i) encode information about an object relative to other landmarks, (ii) integrate newly acquired information

into the map, and (iii) use the map to come up with novel movement strategies (Poucet 1993).

iv. *Social cognition*

Social cognition describes an animal’s ability to recognize, react to, and predict the actions of other individuals (Shettleworth 2010). This form of cognition includes social recognition, social learning, conflict resolution, collective decision-making, and cooperation—skills often considered to be highly complex (Bshary et al. 2014, 2006; Grosenick et al. 2007; Grutter 1999).

Social recognition, or the ability to recognize familiar individuals, has been demonstrated in many fishes (reviewed by Griffiths 2003). Some fishes also use information from conspecifics to inform their decisions concerning mate choice, foraging locations, and antipredator behavior (i.e., social learning; reviewed by Brown and Laland 2003). Intraspecific cooperation, that is cooperation between individuals of the same species, has been shown in a variety of fishes (Balshine and Buston 2008; Brown and Laland 2003; Lindeyer and Reader 2010; Reader et al. 2003). Interspecific cooperation, cooperation between individuals of different species, has also been observed in fishes. For example, grouper *Plectropomus pessuliferus*, and giant moray eels *Gymnothorax javanicus* communicate intentions to jointly hunt. The grouper approaches an eel and performs a distinct head-shake or points its body directly at a prey item that has escaped into a crevice in an attempt to recruit nearby giant moray eels to flush prey out of these crevices and hiding areas (Bshary et al. 2006).

Literature survey of fish cognition studies

While surveying the fish cognition literature on these four key topics, we noticed that most studies were laboratory-based, and conducted on a small number of model species (e.g., goldfish, zebrafish, and guppies). To quantify the extent of this laboratory and species bias, we conducted a systematic literature survey on fish cognition. We first

carried out a PubMed subject search using seven search terms specific to each of the four cognitive areas described above (a full list of search terms used is available in Table 1). Our search was conducted on August 28th, 2019 and based on search terms present in the Article Title, Abstract, or Keywords. This search yielded a total of 2019 results. We then carried out the same search in ISI Web of Science on September 17th, 2019 and this search yielded an additional 449 results. After removing duplicates (i.e., articles that appeared in both our PubMed and ISI Web of Science searches), we scrutinized each article, identified a total of 608 studies relevant to fish cognition, and extracted information from each.

We found a dramatic increase in the number of fish cognition studies over the last decade (68% of the total studies identified were published between 2010 and 2019, Fig. 1a). Cyprinids (e.g., minnows, goldfish) were the most studied fish order (31% of all studies; Table 2). Spatial ability was the most studied of the various areas of fish cognition, while numeracy is the least studied (Fig. 1a). We found that most studies (69%) used captive bred rather than wild fishes (Fig. 1b). We also found that most studies (52%) conducted with sexually mature individuals did not identify the sex of their study specimens (Supplementary Fig. 1). Extremely few studies were conducted in the field; 91% of fish cognition studies took place in a laboratory (Fig. 1c).

Factors compromising our assessment of fish cognition

Our survey confirmed that most fish cognition studies are performed in the lab, use lab-reared animals, and focus on only a few species. There is evidence that these practices can negatively impact our understanding of fish cognition. Next, we summarize this evidence and outline considerations for designing more ecologically relevant studies of fish cognition. The considerations comprise two types or categories of experimental issues: pre-experimental factors and within-experimental factors (Fig. 2). We argue that researchers should consider both these factors when conducting future cognitive studies on fishes and take steps to

Table 1 Keywords used in PubMed and ISI Web of Science literature reviews

Simple learning	Numeracy	Social cognition	Spatial cognition
Simple learning	Numeracy	Social cognition	Spatial cognition
Habituation	Quantity discrimination	Social learning	Navigation
Classical conditioning	Numerical representation	Group decision-making	Orientation
Instrumental conditioning	Number system	Individual recognition	Maze learning
Associative learning	Numerical system	Social recognition	Spatial memory
Avoidance learning	Continuous quantities	Social memory	Spatial learning
Aversive learning	Discrete quantities	Familiarity	Spatial perception

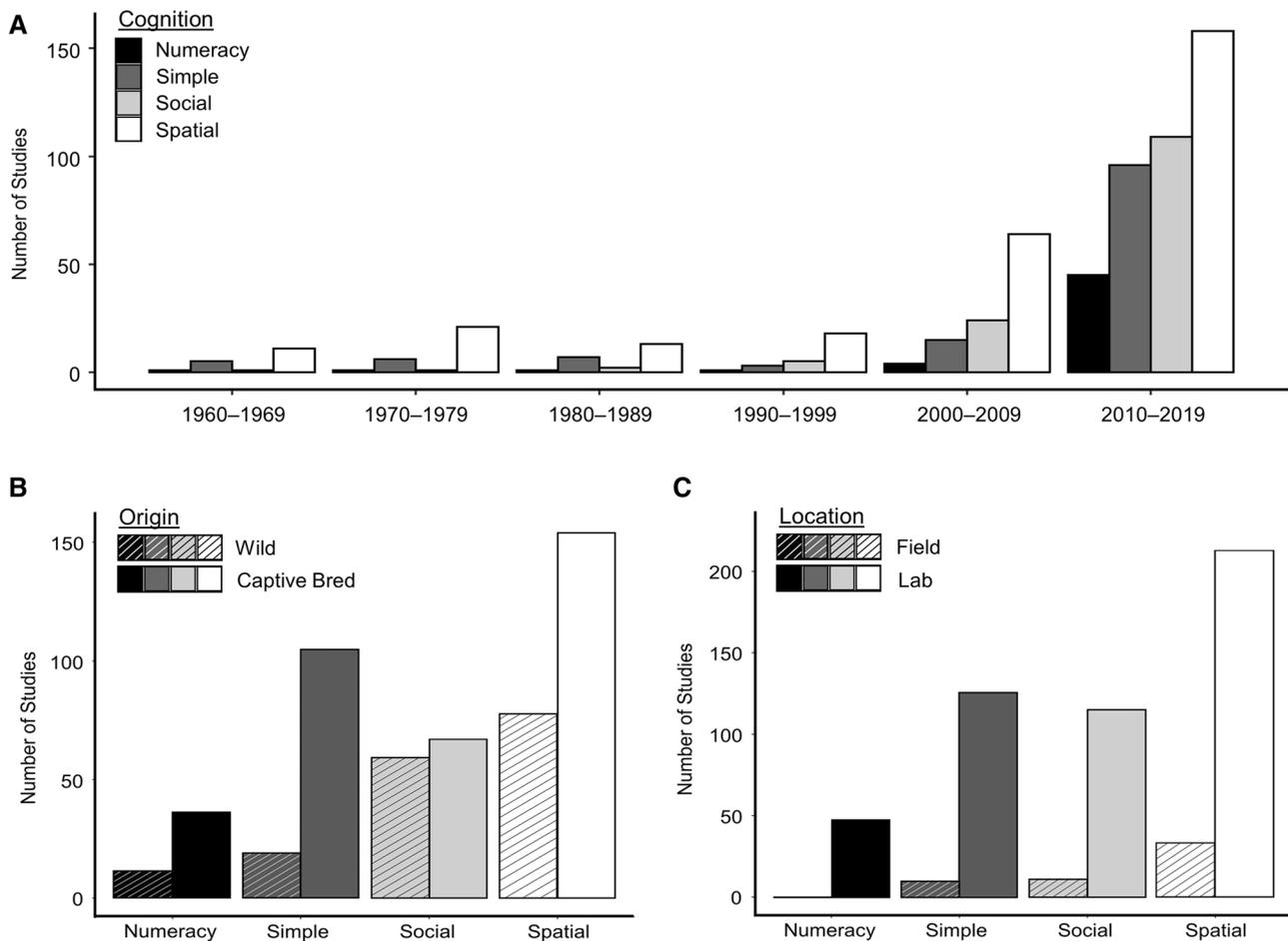


Fig. 1 **a** Peer-reviewed publications since 1960 on fish simple learning as well as numerical, social, and spatial fish cognition. **b** Use of wild versus captive-bred fishes in cognitive studies. **c** Field versus lab-based studies for each type of fish cognition. All figures are based

on our PubMed and ISI Web of Science systematic literature survey (see text for details). Search parameters used to locate papers can be found in Table 1

improve experimental design and laboratory conditions to more closely reflect a species' natural history and behavior. Furthermore, we suggest that conducting fish cognition research in the wild would solve many of these issues, and acknowledge that the combination of laboratory controlled experiments and field-based studies is likely to be the most powerful approach to fully understand fish cognitive abilities.

i. Pre-experiment factors that influence cognition

Selection in captivity

Natural selection operates differently in the lab than in the wild. Captive rearing often provides a benign environment

and limits the strength of natural selection, thus allowing a wider range of phenotypes to persist than would in nature. In some cases, traits suited for life in the wild can be maladaptive in captivity (Courtney Jones et al. 2018; Garner 2005; McDougall et al. 2006). In aquaculture, for example, there may be positive selection on traits such as boldness and aggressive feeding due to high rearing densities, while in nature, these traits could expose individuals to high predation risk (Johnsson et al. 2014; Tave and Hutson 2019). These changes can occur even within a single generation (Christie et al. 2012). Artificial selection in captivity can also affect cognitive performance (Doyle and Talbot 1986; Huntingford 2004; Huntingford et al. 1994). In some cases, this may result from an energy allocation trade-off between brain development versus digestive tract production. Growing quickly makes individuals more competitive in gaining access to food resources (Doyle and Talbot 1986), but can come at the expense of cognitive investment (Stamps 2007;

Table 2 Fish orders as represented in the cognition literature. Papers located were based on PubMed and ISI Web of Science systematic literature review ($n=608$)

Order	Simple	Numeracy	Social	Spatial	Total	Percent of grand total
Anabantiformes	6		2	3	11	2.0
Anguilliformes				7	7	1.2
Atheriniformes	2		1		3	0.5
Beloniformes	1		6	2	9	1.6
Blenniiformes				2	2	0.4
Carcharhiniformes	1		2	10	13	2.3
Characiformes		1		9	10	1.8
Cichliformes	8	9	20	8	45	8.0
Cypriniformes	72	5	21	76	174	30.8
Cyprinodontiformes	13	27	27	24	91	16.1
Gadiformes			1	1	2	0.4
Gasterosteiformes	1	3	17	3	24	4.3
Gobiiformes			2	4	6	1.1
Gymnotiformes	1			9	10	1.8
Heterodontiformes	2				2	0.4
Kurtiformes			1	5	6	1.1
Labriformes				2	2	0.4
Myliobatiformes	1		2	4	7	1.2
Orectolobiformes	3			7	10	1.8
Osmeriformes				1	1	0.2
Osteoglossiformes			2	11	13	2.3
Perciformes	15	2	23	25	65	11.5
Petromyzontiformes				3	3	0.5
Pleuronectiformes				5	5	0.9
Salmoniformes	6		4	21	31	5.5
Scorpaeniformes				5	5	0.9
Siluriformes			1	7	8	1.4
Grand total	132	47	132	254	565	100

Review articles ($n=72$) were removed and studies focusing on more than one fish order ($n=12$) were counted multiple times to cover all the orders represented. The top 5 most prevalent fish orders used for cognition research are identified in bold font

Tsuboi et al. 2015). For example, artificial selection for large brains in guppies, which has been linked to improved cognition (Kotrschal et al. 2013, 2015a), also results in slower growth rates (Kotrschal et al. 2015b) and reduced gut size (Kotrschal et al. 2013). Thus, it seems plausible that inadvertent artificial selection for fast growth rates in captive fishes could also cause declines in cognitive performance, though this possibility has not been well investigated.

Plasticity and the rearing environment

The rearing environment can impact fish behavior long before an experiment begins. Fish cognition is widely thought to be most dramatically influenced by environmental conditions early in development; however, recent evidence suggests that fish brains remain responsive across all life stages (Ebbesson and Braithwaite 2012; Näslund et al. 2012). Both the social and physical conditions that a fish

experiences are known to impact neural development and cognitive abilities.

Chronic exposure to social stress has been shown to decrease neural proliferation (Johansen et al. 2012; Sørensen et al. 2013). While the consequences of long-term social stress on cognitive performance in fishes have not been well studied, most studies to date suggest that social stress impairs learning (Laudien et al. 1986; Olla and Davis 1989; Sørensen et al. 2013). In the cichlid *Cichlasoma paranaense*, isolation decreased performance on an associative learning task (Brandão et al. 2015). Juvenile guppies reared under stressful, crowded conditions were worse at learning from experienced conspecifics how to navigate a maze compared to conspecifics raised at lower densities (Chapman et al. 2008). Cognitive abilities can also be influenced by the conditions experienced early in development or even the conditions experienced by parents (Eriksen et al. 2011; Moore et al. 2019). While no fish studies have directly linked

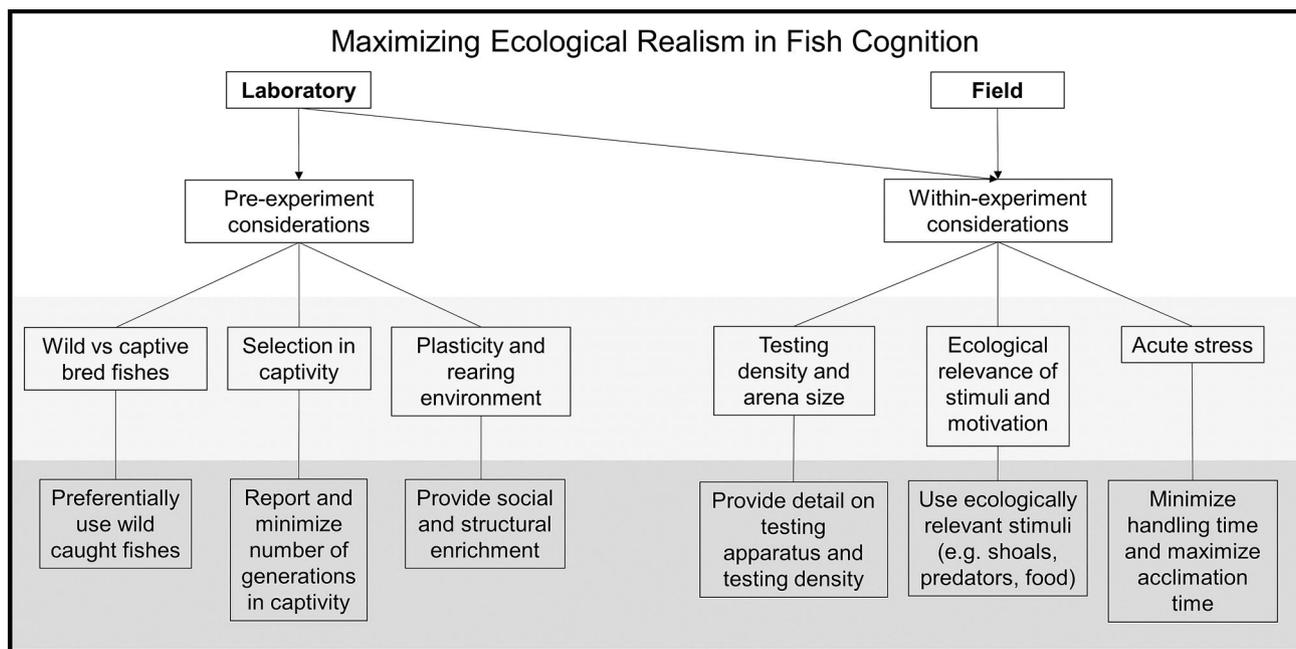


Fig. 2 A concept map depicting the pre- and within-experiment considerations that must be made when designing studies of fish cognition for the laboratory or the field

maternal investment to offspring cognitive abilities, there is evidence in salmonids that cognitively demanding tasks like foraging (Leblanc et al. 2011) and schooling (Tierney et al. 2009) are affected by maternal condition and egg investment. In other animals, such as honeybees *Apis mellifera*, increased maternal investment in workers improved their performance in a later associative learning experiment (Scheiner 2012). In general, our assessment of cognitive abilities in laboratory-raised fishes may be biased by the quality of care received by parents and the conditions experienced during rearing (reviewed by Jonsson and Jonsson 2014; Sørensen et al. 2013). Responses may also be species and/or context specific (Ghio et al. 2016).

The degree of environmental enrichment is considered the primary mechanism for differences in cognitive capacity between captive and wild fishes (reviewed by Näslund and Johnsson 2016). Generally, increased complexity results in enhanced brain growth (Kihlslinger and Nevitt 2006) and faster rates of neural proliferation (Dunlap et al. 2011; Salvanes et al. 2013; von Krogh et al. 2010). For instance, adult zebrafish kept in isolation in structurally enriched environments showed increased telencephalic cell proliferation after only 1 week (von Krogh et al. 2010). These neuro-anatomical differences have been linked to improvements in several aspects of cognition, including foraging on novel prey (Brown and Laland 2003), hiding from predators (Salvanes and Braithwaite 2005), and spatial learning (Salvanes et al. 2013). Interestingly, *Simochromis pleurospilus* cichlids that received variable, sometimes low-ration diets

were cognitively superior to those fed a constant, high-ration amount, suggesting that the cognitive benefits from environmental variability occur even when they result in objective decreases in environmental quality (Kotrschal and Taborsky 2010). While variability in food provisioning might benefit cognition, positive effects of variability are not universal. Thermally stressed female rainbow trout produce offspring with impaired spatial learning abilities and brains with differential expression of important genes for neural development (Colson et al. 2019). Evidence from guppies suggests that even maternal exposure to mild intermittent stress from routine laboratory maintenance procedures, such as twice weekly water changes, can negatively impact associative learning ability in their offspring (Eaton et al. 2015).

The cognitive benefits of enrichment are neither guaranteed nor permanent. In zebrafish, regular exposure to novel objects increased brain growth and associative learning performance, but this effect disappeared in the presence of a mild chasing stressor (DePasquale et al. 2016). Social rearing in captivity increased neural proliferation in the electric fish *Brachyhypopomus gauderio*, but only in brain regions associated with communication, and rates of neural proliferation were still far below those in wild fish (Dunlap et al. 2011). In juvenile Atlantic salmon *Salmo salar*, increases in brain size caused by environmental enrichment were quickly reversed (1 month) when fish were later transferred to bare tanks. In addition, captured wild salmon developed smaller brains in captivity than their wild relatives (Näslund et al. 2012). Thus, habitat complexity seems to matter

for cognitive function in both developing and adult fish. To assess ecologically relevant cognitive abilities of fishes in the laboratory, where structural conditions are almost always simplified compared to those in nature, providing environmental enrichment is therefore important when working with both captive-reared and wild-caught animals.

ii. Within-experiment factors that influence cognition

Testing densities and arena size

Wild fishes almost always experience a bigger social and physical world than those in the laboratory. Generally, fish perform better in the presence of other conspecifics (dampening social isolation stress) and with experienced demonstrators (Brown and Warburton 1999; Lindeyer and Reader 2010; Reader et al. 2003); however, the vast majority of fish used in cognitive studies are tested in isolation. Isolation is known to impair learning (Brandão et al. 2015; Laudien et al. 1986). To induce ‘more natural’ behavior, researchers will sometimes test dyads or trios (Culbert et al. 2019; Silk 2007a, b) and, to reduce social isolation stress, other fish or social companions are often placed behind partitions (Jones and Godin 2009). Despite these practices, it remains unclear whether it is more appropriate to test fish in isolation or test several fish together on any given trial and at the same time, which highlights the difficulty of teasing apart individual from social learning (Brown et al. 2011). Outlining the appropriate social conditions for testing is especially difficult, considering that the effect of social stimulation on performance differs between species. For instance, guppies improved their ability to differentiate quantities when tested in a dyad versus when tested as a singleton (Bisazza et al. 2014), but there was no such improvement in quantity differentiation in dyads versus singleton grass carp *Ctenopharyngodon idella* or Chinese bream *Parabramis pekinensis* (Bai et al. 2019).

Another issue with laboratory-based fish cognition experiments is that these studies are conducted using a wide variety of tank sizes and shapes. In some rodents and birds, individuals can transfer their place-finding ability (spatial cognition) to novel enclosures of different shapes, sizes, and colors (Tommasi and Thinus-Blanc 2004), suggesting that their learning abilities depend on abstract geometric rules rather than the exact structure of the testing apparatus. Fishes also use geometry when solving spatial tasks, and manipulation of the rearing environment can affect spatial performance (Brown et al. 2007; Carbia and Brown 2019). For example, convict cichlids *Archocentrus nigrofasciatus* reared in a circular tank rather than a rectangular tank rely

less on angular geometric cues and more on featural navigation cues (Brown et al. 2007). Typical laboratory conditions also offer less physical space than fishes typically experience in nature, which may impact the cues that are used for navigation. We therefore recommend thoughtful consideration and careful reporting of rearing and testing conditions (e.g., social density, tank size, tank shape, and structural enrichment) in future studies of fish cognition. In general, we recommend the use of the largest housing units and testing arenas that are logistically feasible.

Ecological validity of stimuli and motivation

Animals will respond to stimuli most naturally, and learn associations most easily, when these stimuli have evolutionary and ecological relevance (Dukas 1998; Dukas and Ratcliffe 2009; Garcia and Koelling 1966). However, many fish cognition studies rely on simplistic or unnatural stimuli (e.g., plastic blocks or electrical shocks; Dunlop et al. 2006; May et al. 2016). Stimuli also can vary in terms of their attractiveness and saliency (Millsopp and Laming 2008) and, thus, it is important before starting experiments to determine if the test fish have a pre-existing bias for the stimuli because of its particular color, smell, pattern, or shape (Basolo 1995; Endler and Basolo 1998; Rodd et al. 2002). Another drawback of laboratory experimentation is that stimuli (e.g., food, shelter, predator, competitor, or a potential mate) are typically placed in clear containers or behind glass. Both the focal and stimulus fish often quickly habituate to such barriers, dampening their drive to reach the reward or avoid the unpleasant stimulus (Peeke and Herz 2012). Barriers also reduce the ability to learn by limiting the exploration, sampling, and interaction that can occur (Peeke and Herz 2012). We recommend careful consideration of experimental stimuli to maximize ecological relevance (e.g., use of predator cues instead of electric shocks as aversive stimuli). We recognize that the importance of ecologically valid stimuli may depend on the specific research question, experimental design, and fish species being tested. Some generalist species can perform well under a wide variety of contexts, while other species are specialists that require more specific testing conditions (Del Giudice and Crespi 2018; Ducatez et al. 2015). In fact, the fishes most commonly used for cognitive research to date (e.g., goldfish, guppies, zebrafish, and sticklebacks) are often considered to be generalists; possibly a key factor responsible for their popularity in laboratory studies. However, as comparative cognitive research expands to a diversity of species, we suggest that the ecological validity of experimental setups will be an increasingly important consideration when interpreting cognitive ability.

Acute stress

During most laboratory experiments, researchers stress their animal subjects by capturing, transporting, handling, and/or confining the animal, or by simply placing individuals where they can detect a predator or a competitor. Despite the ubiquitous stress experienced in most experiments, there is little research about how different stressors influence individual learning and how this effect varies across species, sexes, ages, and individuals. In rainbow trout, simulated semi-acute stress (achieved via cortisol implantation) impairs learning and memory (Barreto et al. 2006). Furthermore, when rainbow trout were selected for consistently high or low cortisol responses to stress, the low-responsive group had a longer retention of a conditioned response (Øverli et al. 2004). Individual differences in stress reactivity also impact learning; in many species, bolder individuals learn faster (Mamuneas et al. 2014; Trompf and Brown 2014), perhaps because these individuals will explore and sample more frequently. Precisely, how individual differences in stress responsiveness influences fish spatial, numerical, and social cognition remains to be explored. Despite this uncertainty, we suggest that methodological steps that can reduce stress (e.g., placing cognitive testing apparatus in the home/rearing tank to eliminate handling stress, ensuring that netted fish or transferred fish always remain underwater to eliminate

air exposure) should be employed whenever possible. We also suggest that researchers quantitatively evaluate whether testing protocols allow sufficient time for acclimation to testing arenas. For example, automated tracking (Noldus et al. 2001) can be used to measure when experimental fish return to baseline levels of activity or gill ventilation after manipulation. Similarly, monitoring the concentration of stress hormones (e.g., cortisol) in the blood could provide a physiological indicator that fish have returned to a relatively unstressed state.

The steps toward more ecological relevance in fish cognition studies

Over the past decade, there has been a dramatic increase in the number of studies on fish cognition and, in tandem, a recognition that environmental and developmental factors shape cognition (Webster and Rutz 2020). Both the pre- and within-experiment issues affecting fish cognition studies can be minimized or eliminated using wild-caught fish, by raising fish in enriched environments and using more ecologically relevant stimuli (Fig. 2). Embedding ecology into cognitive research is a necessary next step to understand the evolution and function of fish cognitive abilities, because organisms' neural processes have developed in, and

Steps Towards Ecological Validity

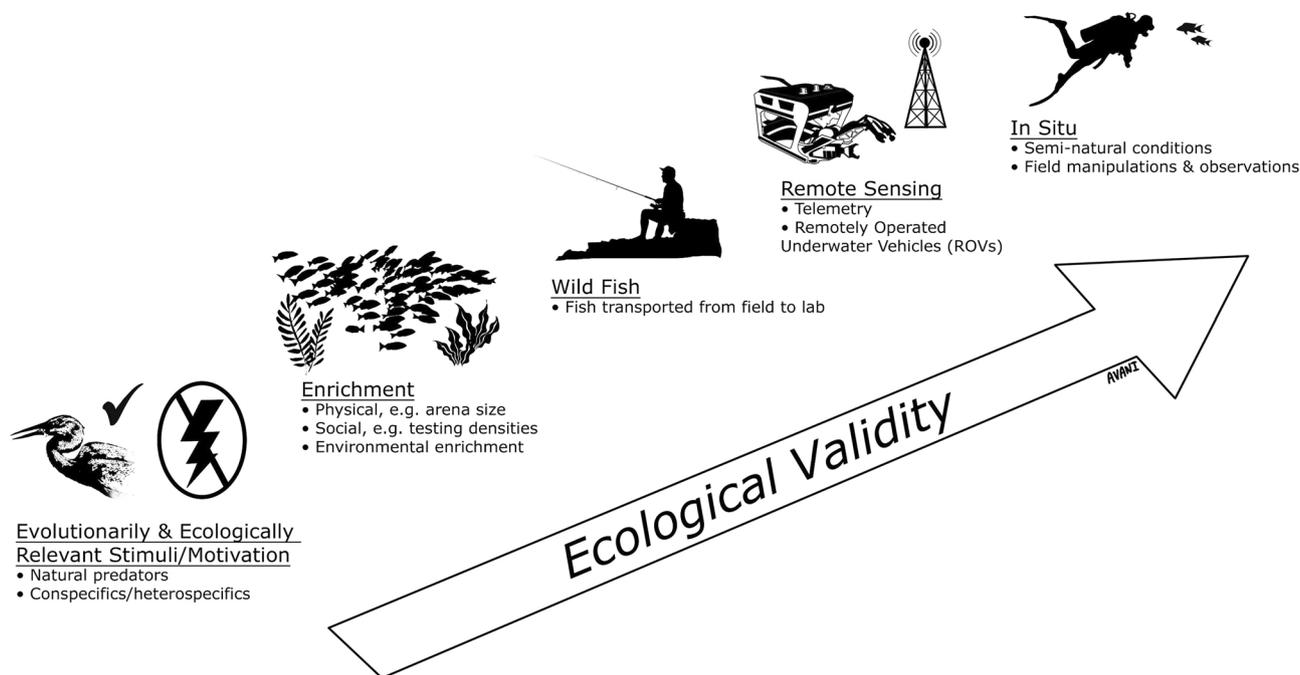


Fig. 3 Considerations for designing more ecologically valid fish cognition studies

are presumably adapted to, their wild environments. We acknowledge that for many fishes, natural history information is virtually non-existent, making it difficult to justify the ecological validity of one experimental design over another. However, we argue that there are some nearly universal steps that can be taken (Fig. 3). For example, laboratory housing is almost always smaller and simpler than conditions in the wild, and thus, cognitive research on fishes would benefit from the use of the largest and most structurally enriched captive conditions that are feasible. Similarly, the use of stimuli with clear ecological relevance (e.g., predators, food, and conspecifics) as opposed to highly artificial stimuli (e.g., plastic blocks, electric shocks) should elicit a more natural response from study specimens and may improve cognitive performance. Given the rapid effects of neural plasticity (weeks–months) and domestication or inadvertent selection (1–2 generations), the use of wild-caught fishes is another solution that is likely to maximize ecological validity of cognitive experiments. In addition to performing more ecologically relevant fish cognition studies in the laboratory, field experiments (whenever possible) could be used to further maximize ecological realism. Although field work often presents additional challenges like long-distance travel, unpredictable weather, and limited control over exogenous factors, there are many benefits. Conducting cognitive research in the wild ensures the use of wild fishes and nullifies selection in captivity. There are also certain behaviors that are best expressed, and therefore best studied, in complex environmental contexts (e.g., problem solving; MacDonald and Ritvo 2016). Technological advancements in telemetry, acoustic receivers, and underwater cameras offer researchers a number of potentially fruitful avenues to explore spatial navigation and social cognition remotely (Ebner and Thiem 2009; Lucas and Baras 2000; Mourier et al. 2017). The manipulation of landmarks and rewards (number or position) is widely used in other taxa (especially with birds and insects) to test both numeric and spatial cognition in the wild (Chittka and Geiger 1995; Helfman and Schultz 1984; Pritchard et al. 2018; Pritchard and Healy 2018; Reese 1989), and shows promise for fish research (see Helfman and Schultz 1984 for a nice example with fish).

To date, there has been a great deal of excellent work conducted on the topic of fish cognition. Our goal is not to discount or diminish this significant and exciting work, but instead to emphasize the complexity of designing high-quality cognitive studies for fishes and to clearly identify the factors that should be considered when planning such research. Our survey demonstrates the paucity of fish cognition field studies (< 10% of studies to date), including their near complete absence from some sub-fields such as numeracy. Our results underscore an overwhelming reliance on lab-based research, and potential confounds spanning from long-term, pre-experimental holding practices to the within-experiment

or immediate effects of ecologically irrelevant tasks. Further studies are still necessary to clarify the full extent of fish cognitive abilities, and we hope that these studies will seriously consider their ecological applicability—as well as the complementary nature of laboratory and field work—and take steps to study fish cognition in more natural settings.

Supplementary file1 (PDF 75 KB)Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10071-021-01488-2>

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Author contributions MGS, AJT, CB, and SB conceived the idea for the review. MGS, AJT, AS, AP, EH, and SB conducted the literature survey and together wrote the first draft of the manuscript. MGS performed the analyses. All authors discussed the results and commented on the manuscript.

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Availability of data and materials Supporting data are available as a supplemental file.

Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

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