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Laterality and fish welfare - A review

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ABSTRACT

Humans interact with fishes in many contexts including aquaculture, scientific study and companion animals. In all of these contexts, fish welfare can be compromised through anthropogenic means. Concern for fish welfare has grown considerably in recent years, with many states and territories now protecting fish through animal welfare regulations. We are not only morally obliged to ensure good welfare of animals in our care, but increasingly required to do so by law. A greater understanding of fish behaviour can lead to the development of welfare indicators. Here we suggest that laterality has wide-spread consequences for fish behaviour and a better understanding of how laterality shapes and interacts with fish behaviour may provide opportunities to enhance fish welfare. Moreover, assessment of laterality through behavioural assays may well be a useful welfare indicator in its own right given the close apparent link between laterality, personality and stress reactivity. Here we review the current research investigating laterality in fishes and highlight instances which may have important consequences for fish welfare.

1. Introduction

Cerebral lateralisation describes an asymmetrical processing of cognitive functions between the two brain hemispheres and most often is overtly displayed as a behavioural bias such as “handedness”. The resulting behavioural bias is known as laterality. Over the last few decades, fish have emerged as arguably the most common taxa used to examine laterality in non-human animals (Bisazza and Brown, 2011a,b). The widespread nature of laterality among vertebrate, and even some invertebrate taxa, hints to this trait being an advantageous evolutionary innovation (Magat and Brown, 2009; Warren, 1980). Benefits associated with laterality include improved cognitive capacity and multitasking capabilities (Rogers, 2000; Vallortigara and Rogers, 2005a). However, despite these associated benefits, studies investigating lateralisation have revealed wide-spread variation within and between populations and contexts (Bisazza et al., 1998; Ferrari et al., 2015; Roche et al., 2020). The existence of such variability suggests that laterality might be under balancing selection, in which there may be contexts that laterality does not provide a fitness benefit or may even be costly (Dadda et al., 2009).

Lateralisation in fishes, has commonly been assessed using a visual task in a detour test (Bisazza and Brown, 2011a,b). This methodology is

typified by an individual repeatedly swimming down a corridor where it is met by an obstacle or stimulus, forcing it to make the decision to make a right or left turn while keeping one eye on the object (Irving and Brown, 2013; Roche et al., 2020). As the optic fields of many fish species do not overlap and the optic nerves are primarily linked to the contralateral hemisphere (Miletto Petrazzini et al., 2020), the direction and intensity of lateralisation can be assessed through their directional behavioural response (Bisazza and Brown, 2011a,b). However, a range of other measures, such as eye preferences when viewing certain scenes (eg conspecifics, predators or novel objects) are also often utilised and usually correlate with the detour test (Sovrano et al., 2001a). Moreover, the lateralised response to a certain object or context appears to be strongly influenced by emotional salience and valence (eg horses; De Boyer Des Roches et al., 2008) and may change over time with experience (Sovrano, 2004). Importantly, many personality traits and emotions, such as aggression and fear, are strongly lateralised. Thus, there appears to be a close link between laterality, personality, emotional reactivity and stress (Byrnes et al., 2016) which may have implications for assessing animal welfare.

Changes in animal behaviour are often the first indicators of changing external or internal factors. Consequently, behavioural responses represent key indicators of fish welfare (Martins et al., 2012).

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Classic welfare indicators including changes in swimming behaviour, aggression and ventilatory activity, amongst others, have all been shown to be key predictors of an individual's stress level and, thus, overall welfare status (Martins et al., 2011a). Laterality may shape or be associated with any of these behavioural indicators. Given the generally simple methodologies which can be employed for the assessment of laterality, and the impact of various ecological and stress factors on laterality, there is a growing interest in the use of laterality in assessing fish welfare. In this review, we examine the role of laterality in shaping fish behaviour and, in doing so, highlight contexts that may aid fish welfare practices. We also discuss the potential use of laterality, and associated behaviours, as an indicator and assessment tool for fish welfare.

2. Fish welfare

Since the 1960's there has been a growing push from the general public to respect the welfare of animals in food production systems, as companion animals and in scientific research. Fish held in captivity are frequently exposed to stressors, through processes such as crowding, handling, grading and transportation (Eissa and Wang, 2016; Wilkinson et al., 2006).

However, fishes have rarely been considered part of our moral circle (Brown, 2015) reflected by the fact that they are frequently excluded from animal welfare legislation around the world (Brown and Dorey, 2019). In many states and territories in Australia, for example, fishes are specifically excluded from the definition of an 'animal' in animal welfare legislation. Over the last few years, however, this situation has started to change, and it may well be associated with the growth of the aquaculture industry. More fishes for human consumption are now produced in aquaculture than are captured by wild fisheries (FAO, 2020), meaning that intensive production of fish is now at a similar intensity to that of terrestrial farm production. Moreover, according to Fish Count UK (fishcount.org.uk: towards more humane commercial fishing) somewhere between 1 and 3 trillion individual fish are captured and killed annually by commercial fishing operations. Fishes are also the most abundant pets in the world and are being increasingly used for scientific research, ranked second after rodents (Brown and Dorey, 2019). In short, the scale of the welfare problem faced by fishes is considerably greater than all the terrestrial animals commonly used by humans combined.

Simultaneous to these welfare developments, our understanding of the cognitive complexity of fish has grown tremendously (Brown et al., 2011; Sneddon and Brown, 2020; Vila Pouca and Brown, 2017) and it is now widely recognised that fishes have the capacity to suffer (Aas et al., 2020; Kristiansen and Bracke, 2020; Sneddon, 2015). This growing body of research combined with shifting consumer expectations has led the European Union to take a firmer stance on the topic of fish welfare and there are several new legislative frameworks that protect fish welfare in member states (eg European Commission and European Food Safety Authority). Similar stances have been adopted within the scientific community (Huntingford et al., 2006; Sloman et al., 2019). In addition, welfare certifiers have recognised the sea change in public perception and are rushing to provide certification standards for fish welfare on food products (eg <https://www.asc-aqua.org/>, Global Aquaculture Alliance, 2017; RSPCA, 2018a; RSPCA, 2018b etc). Whilst these certification standards differ in their approach, they generally focus on consideration of the 'five freedoms': freedom from hunger/thirst, discomfort, pain/injury/disease, fear/distress and the freedom to express normal behaviour (Farm Animal Welfare Council, 2009). In all cases, behaviour and physiology play key roles in identifying poor welfare and are frequently used as indicators in animal welfare standards. The welfare of fishes has received increasing consideration in recent years, with notable changes in aquacultural production processes and end-product quality (Chandross et al., 2004; Huntingford et al., 2006). In many cases, laterality and related processes are involved but laterality is seldom incorporated in fish welfare assessment.

2.1. Laterality and sociality

Many fish species demonstrate some form of sociality during their lifetime, from complex social structures found in some species of cichlids (Limberger, 1983) to simpler forms such as temporary aggregations in the presence of predators or around food resources (Magurran, 1990). The formation of groups allows fishes to benefit from the selfish herd (Hamilton, 1971), risk dilution (Foster and Treherne, 1981) and confusion effects (Landeau and Terborgh, 1986; Penry-Williams et al., 2018). However, when living with limited resources, group living can also become an impediment, resulting in an increase in competition, aggression and pathogen transmission (Jobling and Koskela, 1996; Martin et al., 2012; Ward et al., 2006a,b). The contests that result from competition can give rise to the formation of dominance hierarchies. Social relationships within groups of fishes can be complex and there is growing use of network analyses to quantify these relationships (Croft et al., 2005). Recent advances in analytical techniques combine elements of network analysis as well as hierarchy components (Cumming, 2016; Pini-Fitzsimmons et al., 2020). To date, no studies have examined if laterality shapes social network structure.

Social interactions are not just an important part of a species' ecology and evolution, but they are also essential for good animal welfare, with social isolation and reduced social interaction profoundly negatively impacting the physiology and health of some fish species (Forsatkar et al., 2017; Giacomini et al., 2014). Similarly, aggression between conspecifics can arise in some species if appropriate social densities are not maintained (see 2.1.3 below). The relationship between stocking density and aggression in captivity varies between species (Manley et al., 2014) and is a primary fish welfare concern (Bergqvist and Gunnarsson, 2013).

The link between laterality and sociality in fishes is firmly established, with fish species found to have a preference for either right or left eye-use during social interactions (Reddon and Balshine, 2010; Roux et al., 2016), with directional preference differing even between closely related species (Sovrano et al., 2001b). However, the ecological relevance of laterality in social interactions changes depending on whether it is found at the individual or population level (Vallortigara and Rogers, 2005b). Laterality at the individual level refers to an individual demonstrating an asymmetry in one or more behaviours (Vallortigara and Rogers, 2005b). Many studies have identified individual-level laterality but failed to find a global tendency in one specific direction at the population level. A study on goldbelly topminnows (*Girardinus falcatus*), for instance, found that while the individuals had a right or left preference for viewing a social stimulus, there was no bias at the population level (Dadda et al., 2012). Laterality at the population level, however, refers to the presence of a behavioural laterality preference in a consistent direction across the majority of a population. It has been suggested that lateralisation could arise at the population level as a form of evolutionary strategy when the costs of being predictable and behaving sub-optimally are compensated by the advantages of being synchronised with the other individuals of the population (Brown, 2005; Frasnelli and Vallortigara, 2018). In essence, social behaviour may be a driving force behind the evolution of laterality. In fishes this is particularly relevant in the context of schooling behaviour (see 2.1.2 below).

2.1.1. Laterality and conspecific recognition

In a wide range of vertebrates there is a tendency to use one or the other eye when viewing conspecifics (Vallortigara and Andrew, 1994) which likely has implications for animal welfare. In mammals, for example, mothers may keep their offspring on the left (whales; Karenina et al., 2010), horses; Karenina et al., 2018 and humans; Todd and Banerjee, 2016) so the mother can monitor their child with the right hemisphere which is specialised for attention and emotional processing. To our knowledge no such investigations have examined this in the context of fish parental care despite parental care being commonplace in many fish species (Balshine, 2012). Sovrano et al. (1999; 2004) suggest

fish process social stimuli preferentially with their right hemisphere, (Sovrano et al., 1999; Sovrano, 2004) though this directional preference can differ even within the same taxonomic family (Fuss et al., 2019) and between different sexes (Reddon and Balshine, 2010).

Fishes differentiate between familiar and unfamiliar individuals, and they prefer to school with the former (Griffiths, Siân and Magurran, 1997). When facing a familiar or unfamiliar conspecific, ricefish (*Xenopoeilus sarasinorum*) look at the former with their left eye, while the right eye is used to check for possible dangers coming from unfamiliar stimuli (Sovrano, 2004). Interestingly, the hemisphere used to examine unfamiliar individuals may shift over time as individuals become acquainted to a social stimulus (Sovrano, 2004). Shoals of fish comprised of familiar individuals have enhanced foraging, anti-predator behaviour and social learning capacity (Griffiths, 2003) all of which can have implications for aquaculture and the aquarium trade.

2.1.2. Laterality and swimming/schooling behaviour

Acute and chronic stressors in aquaculture cause changes to both individual and group swimming behaviour, and evidence suggests that swimming behaviours can be used as indicators of fish welfare (Damsgård, 2008; Martins et al., 2011b). There are many assays for assessing laterality in fishes, but the predominant methodologies examine swimming behaviour by either assessing swimming direction in a circular arena (Bisazza, 1996; Dale Broder and Angeloni, 2014; Izvekov et al., 2014) or turn direction choice in a detour test (Irving and Brown, 2013; Roche et al., 2020). In addition, laterality at the population level may have emerged in social groups to increase synchrony in behaviour (ie schooling; Brown, 2005). Thus, there are many contexts in which both physical and cognitive laterality at both the individual and population levels is important in shaping swimming behaviour in fishes.

While researchers have often found that fish demonstrate strong directional preferences, the idea that morphological asymmetries can be causally linked to behavioural asymmetries has been studied in only a few species. Behavioural laterality in swimming direction, for example, has been linked to morphological asymmetries of the frontal bones in roach (*Rutilus rutilus*) (Izvekov et al., 2012). Several papers have examined the relationship between habenular nucleus asymmetry and lateralised turn preferences in fishes, including pearl cichlids (Reddon et al., 2009), convict cichlids (Gutiérrez-Ibáñez et al., 2011) and zebrafish (Dadda et al., 2010a,b). Interestingly, the relationship between habenula asymmetry and turn bias appears to be reversed between male and female convict cichlids (Gutiérrez-Ibáñez et al., 2011). In the poeciliid, *Girardinus metallicus*, the directional bias for right or left turns in a detour test positively correlate with head incline asymmetry, but negatively with a fast-escape response test (Matsui et al., 2013). Fast-start startle responses are controlled by the mauthner neurons and several studies have revealed that the direction of the startle response is correlated with the size of the mauthner neuron on the left of right side of the body (eg Moshkov et al., 2009). Dadda et al. (2010a,b) for example found that strongly lateralised fish showed higher escape reactivity

In addition to the studies investigating physical lateralisation on swimming behaviour, there is growing evidence that lateralisation can impact schooling behaviour. In general, it is hypothesised that population level laterality may emerge as an evolutionary stable strategy in social contexts due to a need to increase synchrony within groups of animals to further gain from the confusion effect (Brown, 2005; Val-lortigara and Rogers, 2005b). The increased predation risk associated with the oddity effect is a related mechanism ensuring that members of a school look and behave similarly (Penry-Williams et al., 2018; Theodorakis, 1989). The highly synchronised behaviour of fish schools is a testament to the importance of such effects. Fusilier (*Caesio teres*) demonstrated improved individual escape performance when having the same turning preference as the majority of the school, with the degree of population-level laterality increasing along with the perceived predatory risk (Chivers et al., 2017). While there are costs to being

strongly lateralised (eg predictable behavioural responses to predators) the benefits associated with laterality, particularly in social animals, clearly outweigh them in these contexts.

In fishes, laterality has been found to improve schooling behaviour by increasing cohesion and alignment between individuals (Bisazza and Dadda, 2005) and influencing schooling geometry (Bibost and Brown, 2013). There is no doubt that exposure to predation threat during development can shape laterality but there is also an underlying heritable component (Bisazza et al., 2000; Brown et al., 2007). Bisazza et al. (2000) studied 16 species of fish and found that shoaling species were more likely to present laterality at a population level in predator escape response, while non-shoaling species had the tendency to develop individual lateralisation (Bisazza et al., 2000). Bishops (*Brachyrhaphis episcopi*) from high predation locations which show strong schooling behaviour are more strongly lateralised than those from low predation areas where schooling is not a priority (Brown et al., 2004). Lateralised guppies (*Poecilia reticulata*) have better discrimination between different sized schools of conspecifics compared to non-lateralised individuals (Gatto et al., 2019). Lateralised yellow-eyed mullet (*Aldrichetta forsteri*) occupy the safest part of the school compared to control fish (Middlemiss et al., 2018). Similarly, lateralised rainbowfish (*Melanotaenia* spp.) tended to adopt positions in the school that corresponded with their dominant eye for viewing conspecifics (Bibost and Brown, 2013). Collectively, there is strong evidence of the role of laterality in shaping synchrony in fishes particularly in high predation environments.

In aquaculture, pens often induce circular swimming patterns, such as those seen in Atlantic salmon (*Salmo salar*) (Johansson et al., 2007). Constant swimming is necessary to facilitate this species' migratory nature (Martin et al., 2012; Sutterlin et al., 1979), but it may be important for fish to all be synchronous in their directional preference (clockwise or anti-clockwise) to minimise collisions with other individuals and the cage itself (Føre et al., 2009; Iwama, 2007). However, as outlined above, there seems to be variation in the preferred schooling position, with individual preference for conspecifics on a specific side (left or right side) and turn direction, which may generate within-group conflict (Bibost and Brown, 2013). An inability to adopt a preferred location within a school could cause stress and anxiety, in addition to the typical stressors associated with fish farms. It would be interesting to determine if turn preferences in this circular swimming context have been incidentally artificially selected within aquaculture strains to increase school direction cohesion as has been hypothesised in the wild context (Brown, 2005).

2.1.3. Laterality and aggression

Aggressive interactions between members of conspecifics have also demonstrated behavioural laterality in many taxonomic groups such as bees (Rogers et al., 2016), fish (Ariyomo and Watt, 2013), reptiles (Deckel, 2005), birds (Anderson et al., 2010) and mammals (Austin and Rogers, 2012). Fish show both individual- and population-level laterality in their eye preference during aggressive interactions, depending on the species. Bisazza and De Santi (2003) found a right bias while studying three species of teleosts (*Gambusia holbrooki*, *Xenotoca eiseni* and *Betta splendens*), while a study on zebrafish (*Danio rerio*) found a tendency in using the left eye, with sex influencing the strength of the lateralisation (Ariyomo and Watt, 2013). These species-specific characteristics could be an important consideration when investigating laterality and fish well-being. This is particularly relevant for highly aggressive or territorial fish, such as the Siamese fighting fish (*Betta splendens*). This species is very popular in commercial aquarium trade, while in natural environments it has become increasingly endangered (Sermwatanakul, 2019). Many studies have shown that aggressive behaviour in fighters is highly lateralised at the individual-level (Cantalupo et al., 1996; Takeuchi et al., 2010). Since this species is often reared in confined spaces in farms and aquarium retailers (Sermwatanakul, 2019), selecting certain individuals to house together by considering eye preference could potentially lead to less stress and

injuries for the individuals, improving not only fish welfare but, in theory, revenues for producers. While fighters were originally bred for their aggression, it may be possible to select for less aggressive individuals which would be more suited to a community aquarium. Laterality could be used as a simple assay to judge aggression and in sorting individuals into behavioural categories prior to distribution or breeding.

2.2. Laterality and foraging behaviour

While behavioural laterality may have evolved as an anti-predatory mechanism (Magurran, 1990), it has also been found to be associated with competitive advantages in foraging efficiency (Jolles et al., 2017; Pajmians et al., 2020). The scale-eating cichlid (*Perissodus microlepis*), is perhaps the best studied example of laterality in foraging behaviour. This fishes' morphological asymmetry in its mouth parts is associated with a preference to attack prey on one side or the other (Lee et al., 2012). Interestingly, morphological bias develops along-side the behavioural one through learning (Takeuchi et al., 2016; Takeuchi and Oda, 2017). Dadda and Bisazza (2006b) have also found that lateralised female topminnows were better at foraging whilst simultaneously attending to male harassment. Similar results have been found in a predation context where lateralised fish could better track predators and forage simultaneously (Dadda and Bisazza, 2006a). Lateralised individuals managed to capture twice as many prey items as non-lateralised individuals in the presence of a predator whereas there was no difference in the absence of a predator. A study examining the hunting behaviour of the sailfish (*Istiophorus platypterus*) found that most individuals had a preference for attacking the prey from left or right, but left and right individuals were equally present in the population (Kurvers et al., 2017). These results are indicative of the typical sorts of dual problem-solving benefits that laterality often infers as well as the inherent variability one often finds within populations (see section: 2.4).

Selecting for laterality in certain aquaculture species could be an important factor in securing high foraging efficiency for the fish alongside enhanced schooling behaviour, leading to both a better welfare for the fish (a better social environment), and improved outcomes in terms of for the fish farm (eg reduced stress and enhanced feed conversion). Further research is needed to examine the impacts of laterality in aquaculture conditions.

2.3. Environmental impacts on laterality

A number of environmental factors, such as physical environmental complexity and predation pressure have been shown to alter laterality in fishes during ontogeny. Changes of carbon dioxide concentrations and associated changes in water acidity can also impact a fish's laterality (Lopes et al., 2016), which may have unforeseen impacts on fish behaviour in both natural populations and those in aquaculture in near future global warming scenarios (Cattano et al., 2018). The mechanisms of laterality plasticity are not entirely understood but likely involve neurological and physiological changes. Some of these factors may require an individual to acquire improved cognitive capacity and multitasking capabilities to increase the chance of survival in these contexts (Brown and Braithwaite, 2005; Rogers, 2000; Vallortigara and Rogers, 2005b). For example, exposure to predation can cause increased stress (Archard et al., 2012; Bell et al., 2010), with even indirect exposure to predator (predator odours) leading to behavioural changes (Siepielski et al., 2016). There appear to be multiple links between laterality and stress reactivity (see 2.6 below). Environmental factors may also influence hormone production such as testosterone, which can also shape laterality (Schaafsma and Groothuis, 2011). Ocean acidification, on the other hand, seems to alter the function of GABBA-A receptors (Nilsson et al., 2012).

Exposure to predation has profound impacts both on the evolution and development of laterality. Predators have a strong influence on both the strength and the direction of individual laterality in the poeciliid,

Brachyraphis episcopi, with predator-naïve fish having lower levels of laterality than predator-exposed ones (Brown et al., 2004). However, laboratory reared fish altered both the strength and direction of their laterality following repeated chasing with a net (Brown et al., 2007). Similar results were also found in the guppy, where exposure to predator's chemical cues induced the development of lateralisation (Dale Broder and Angeloni, 2014). Studies following this also found perceived predation risk to increase laterality strength in a matter of days (Ferrari et al., 2015) regardless of the risk level experienced during development (Dale Broder and Angeloni, 2014). Bisazza et al. (2010) also found evidence of maternal effects, with offspring from females exposed to predatory threat demonstrating stronger lateralisation in both visual and motor assays. Work by Schaafsma and Groothuis (2012) suggests that at least one possible mechanism through which maternal effects may operate is via maternal hormones. While Ambon damselfish (*Pomacentrus amboinensis*) experiencing increased perceived risk during certain times of the day, also demonstrated increased strength in lateralisation during these times (Ferrari et al., 2017). Clearly, this degree of plasticity in the development of laterality has fitness benefits. Lateralised shiner perch (*Cymatogaster aggregate*) for example, demonstrated improved escape performance and reactivity when exposed to a simulated predator attack compared to their non-lateralised conspecifics (Dadda et al., 2010a,b). Collectively, these results suggest that lateralisation has both heritable and experience-based component, the latter of which suggests that it may be a useful assay to assess welfare.

In addition to predation pressure, other environmental stressors, such as increased CO₂ levels can impact laterality and has been particularly well studied in coral reef fishes (Domenici et al., 2012, 2014). This has also been evidenced in temperate species, with increased CO₂ producing lower levels of absolute lateralisation in three-spined sticklebacks (*Gasterosteus aculeatus*) alongside a reduction in exploratory behaviours, boldness and learning capacity (Jutfelt et al., 2013). Similar to chicks (Rogers, 1990), variable exposure to light also influences the development of lateralisation in fishes. Zebrafish exposed to differing light levels during early development produced differences in laterality, in addition to personality traits including activity, sociality and boldness (Andrew et al., 2009; Budaev and Andrew, 2009; Sovrano et al., 2016). Similar results have also been found in goldbelly topminnows (Dadda and Bisazza, 2012). Both strength and direction of lateralisation in turn bias was found to be influenced by physical environmental complexity in the crimson-spotted rainbowfish (*Melanotaenia duboulayi*), with the direction of the trend reversed by sex. More enriched environmental rearing conditions led to strongly lateralised behaviours in males, with the opposite pattern identified in females (Bibost et al., 2013a,b). Similar to its role in schooling and predator avoidance, the advantage of a lateralised brain in complex environments is likely an adaptation related to processing multiple stimuli simultaneously.

Many studies have shown an improvement in the performance of hatchery-reared fish by enriching the rearing environment (Arechavala-Lopez et al., 2019; Braithwaite and Ahlbeck Bergendahl, 2020; Mazzola et al., 2000; Näslund and Johnsson, 2016), with the degree of enrichment playing a significant role (Zhang et al., 2019). Previous work has shown that environmental enrichment can enhance laterality in fish (Bibost et al., 2013a,b) resulting in bigger brain sizes (Kihlslinger and Nevitt, 2006; Näslund et al., 2012) and is linked to better cognitive performance (Salvanes et al., 2013). It seems likely that rearing fish in mundane environments may have multiple impacts on fish cognition which could be one of the causes of the documented reduction of survival of hatchery-reared fish when released in the environment (Brown and Laland, 2001; Brown and Day, 2002; Tsuboi et al., 2019). Assaying hatchery fish for laterality may be a rapid way of testing if they are suitable for release into the wild, particularly for the conservation of rare and endangered species (Fraser, 2008; Philippart, 1995).

2.4. Laterality and cognition

Laterality being such a widespread behavioural trait strongly suggests it has fitness advantages, many of which seem to be related to cognitive function. It is generally believed that the development and evolution of lateralisation is an advantageous mechanism that improves cognitive capacity and multitasking by allowing for the processing of multiple external stimuli (Brown, 2005; Vallortigara and Rogers, 2005b). Dadda and Bisazza (2006a) explain that lateralised fish may keep track of the predator with one eye and process this information in the opposite hemisphere, allowing for the processing of other tasks, such as schooling or foraging, with the remaining hemisphere. Non-lateralised individuals by comparison tend to switch between tasks and use both eyes. In guppies, lateralisation enhances the numerical skills (Dadda et al., 2015; Gatto et al., 2019) while lateralised female topminnows are more efficient than non-lateralised individuals in foraging while avoiding a harassing male (Dadda and Bisazza, 2006b). Sticklebacks experiencing monocular eye-use through eye occlusion outperformed control binocular eye-use individuals in quantity discrimination of school size, particularly for left-monocular individuals (Mehlis-Rick et al., 2018). Left-aligned rainbowfish (*Melanotaenia duboulayi*) outperform right-aligned conspecifics in a classical conditioning experiment (Bibost and Brown, 2014). However, such advantageous cognitive skills in association with laterality are not always consistently identified. Lateralised fish, for instance, do relatively poorly when learning to navigate a radial maze because they are handicapped by underlying turn biases (Brown and Braithwaite, 2005). Dadda et al. (2009) found non-lateralised goldbelly topminnows outperform lateralised individuals in both bilateral shoal choice and in finding the centre of a figure than lateralised individuals. Similarly, lateralised damselfish (*P. amboinensis*), perform better while foraging under predatory pressure, however, they were outperformed in aggressive social interactions to establish dominance by non-lateralised individuals (Chivers et al., 2017). Collectively these studies suggest that there are circumstances in which laterality may be detrimental to an individual.

It is interesting to note that environmental enrichment can not only enhance laterality (Bibost et al., 2013a,b), but it can also increase brain size and cognitive function (Salvanes et al., 2013). The apparent syndrome linking laterality, personality, cognition, brain size and stress reactivity is certainly of interest from a welfare perspective and is somewhat reminiscent of domestication syndromes first identified by Darwin (Wilkins et al., 2014). This syndrome could be manipulated perhaps by altering rearing conditions to promote the development of certain beneficial behavioural types to suit captivity (Bisazza and Brown, 2011a,b). This plasticity could be further reinforced by selective breeding of particular lines (Bisazza et al., 2007). Although there is some argument that fish species that are already suited to life in captivity should be targeted for aquaculture production, humans have a long history of selectively breeding for domestication.

2.5. Laterality and emotion

Fish welfare parameters generally fall into function-based categories, revolving around biological functioning and physiological stress response (Duncan, 2005; Martins et al., 2011b). While feeling-based definitions of fish welfare relate more to the emotional state of an individual (Duncan and Dawkins, 1983; Martins, Castanheira, et al., 2011). Recent work has also begun to investigate the role of emotions in fish behaviour (Braithwaite et al., 2013; Brown and Dorey, 2019; Cerqueira et al., 2017; Kittilsen, 2013). Panksepp (1998) defines emotions as 'processes which are likely to have evolved from basic mechanisms that gave animals the ability to avoid harm or punishments and to seek valuable resources or reward'. Crump et al. (2020) offer a similar definition: 'short-term states elicited by stimuli that animals will work to acquire or avoid'. Even since Darwin (1872), scientists have viewed emotions as important functional drivers of animal behaviour and thus

subject to natural selection and a product of evolution. Operationally, positive valence refers to high arousal stimuli initiate the reward acquisition system, whereas negative valence describes high arousal stimuli operating the punishment avoidance system.

Objects and contexts in the world around us vary in their salience (arousal or emotional intensity) and emotional valence (positive or negative). These values are often set by experience, with novel objects being inherently neutral or possibly even negative, if they are perceived as potentially threatening (neophobia). Research on humans have found links between cognitive state and affective states, with emotional states impacting an individual's assessment and decision-making process (cognitive bias; Haselton and Nettle, 2006). Similar processes have been found in a wide range of non-human animals (Harding et al., 2004; Mendl et al., 2009) including fishes. Atlantic Salmon (*S. salar*), for example, become more aggressive and show outward signs of distress when feeding times became more unpredictable; akin to frustration in humans (Vindas et al., 2012). A number of fish suffer from winner and loser effects if they repeatedly win or lose aggressive encounters (Oliveira et al., 2011). While non-lateralised rainbowfish demonstrated bolder risk-taking behaviours than strongly lateralised fish, suggesting that as stress or fear is intensified, it is primarily processed by a single hemisphere (Brown and Bibost, 2014).

In non-human animals, numerous studies have identified differential processing of positive and negative stimuli between the hemispheres. The emotional valence hypothesis predicts that positive emotions are analysed with the left hemisphere while the reverse is true for negative emotions (Demaree et al., 2005). Rogers (2010) described the differing functionality of the two hemispheres in relation to laterality with the right hemisphere appearing to be more associated with timorous and aggressive behaviours, while the left hemisphere seems to be more associated with calmer and more exploratory behaviours. Gainotti (2019), on the other hand, suggested that the right hemisphere is dominant for emotional activity, regardless of affective valence. All three perspectives have a common theme in that emotional stimuli tend to be lateralised between the two brain hemispheres.

Lateralisation of fear response is common in many vertebrates, including many different species of fish, although inter-species differences in the hemisphere used for processing emotion have been identified (Leliveld et al., 2013). In fishes, this relationship seems to be variable, with inconsistency in the actual hemisphere involved in processing negative or positive stimuli. A seminal study by Bisazza et al. (2000) analysed directional turning bias when approaching a negative stimulus, a net the fish learned to consider a threat, for 16 species of fish. The results showed a clear turning bias in most of the species, with the left or right preference related to their phylogenetic relationships (Bisazza et al., 2000). Fish examining familiar, non-threatening stimuli may also show a bias in the eye they view the object with and analyse the information using the contralateral hemisphere (Sovrano et al., 1999). When observing conspecifics (positive valence), for example, bishop used one eye, while they used the other eye to view a novel object (negative valence) (Brown et al., 2007). Using a combination of behavioural and cognitive approaches, a study on pigs found that covering one eye or the other could change the animal's reaction of subjects towards objects that had been previously associated with negative or positive outcomes (Goursot et al., 2019). Similarly, Convict cichlids (*Amatitlania nigrofasciata*) exposed to alarm cues (negative stimulus) changed eye-use, a proxy for cerebral hemisphere use, from a right to a left bias (Moscicki and Hurd, 2017). However, a multi-species study (*Gambusia holbrooki*, *Xenotoca eiseni* and *Betta splendens*) identified the opposite pattern when processing negative social stimuli, such as aggression (Bisazza and De Santi, 2003). Assessing emotional responses is clearly a useful tool in the context of animal welfare (Boissy et al., 2007) but has not been well utilised in fishes to date (Cerqueira et al., 2017).

Cognitive bias has been used to assess welfare in farm and companion animals for some time where it is assumed that animals suffering

from poor welfare will have a pessimistic outlook (Mendl et al., 2009). There is increasing interest in using cognitive bias tests to assess fish welfare (Wojtas et al., 2015) but this is still in its infancy. Cognitive bias would be relatively easy to test in fishes based on existing protocols used for assessing other animals (Harding et al., 2004), in which subjects are trained to associate one stimulus with a positive reward (e.g. food) and another with punishment (e.g. shock) or no reward. Cognitive bias influences the decision-making process when subjects are then presented with an ambiguous stimulus; pessimistic individuals will avoid the ambiguous cue whereas optimists will approach it expecting to be rewarded. The methodological approach of emotional conditioning standardises the emotional contexts because it permits the use of the same stimulus (eg a novel object) for testing negative and positive emotional processing thereby controlling for underlying inherent bias (Bisazza et al., 2000).

2.6. Laterality and coping styles

External stressors, defined as environmental changes impacting the homeostasis of an individual, can vary greatly in their nature and impact (Daskalova, 2019). Stress can be induced both physically and psychologically. The presence of such a stressor, be it acute or chronic, may illicit reactions from the individual which can cause behavioural or physiological responses deleterious to health or animal welfare (Daskalova, 2019; Martins et al., 2012; Tort, 2011). Hormonal response is a key player in the maintenance of internal homeostasis and the expression of a stress response. As such, the Hypothalamic-Pituitary-Interrenal (HPI) axis holds a pivotal role in the endocrine stress response in most teleost fish species, with raised levels of catecholamines and corticosteroids often used as a key indicators of acute stress in aquaculture (Barton, 2002; Barton and Iwama, 1991; Øverli et al., 2004). However, chronic stress from life in captivity can also present as lower levels of stress hormones compared to wild fish when subjected to acute stress (Awata et al., 2011; Douxfils et al., 2011; Mazur and Iwama, 1993). Hence measuring stress hormones alone may lead to imprecise recognition of welfare problems which is why a number of welfare indicators are typically employed (Noble et al., 2018). Given the heavy physiological response many stressors illicit on an individual, compensatory behavioural and physiological responses to help an individual cope with deviations from homeostasis usually occur (Pavlidis et al., 2015; Theodoridi et al., 2017). These responses can be useful secondary indicators of poor welfare.

Koolhaas et al. (1999) defined behavioural responses to external stressors as ‘coping styles’; A consistent set of behavioural and physiological stress responses demonstrating repeatability and distinctiveness to groups of individuals. Two general strategies in response to aversive (Koolhaas et al., 1999). While other work investigating personality has included the consistency or repeatability of individual behavioural traits over time or across contexts (Budaev and Brown, 2011), the idea of coping styles aims to explicitly address and include changes under stressful and hostile environments (Koolhaas, 2008; Koolhaas et al., 2007; Øverli et al., 2007). At a behavioural level, proactive coping styles are characterised by bolder, more aggressive, dominant and exploratory behavioural traits to actively counter the stressful stimuli. While a reactive coping mechanism is typical of shy personality types, characterised by immobility and low levels of aggression (Millot et al., 2014; Øverli et al., 2006; Schjolden et al., 2005; Vindas et al., 2017). There are also a number of physiological differences, most notably higher activation of the HPI-axis system in reactive coping style individuals, while proactive individuals have lower HPI axis reactivity and generally lower basal concentrations of glucocorticoids (Øverli et al., 2007). Proactive fish are generally able to recover faster from stressful events (Ward et al., 2006a,b), exhibit lower susceptibility to diseases (MacKenzie et al., 2009) higher growth rates (Basic et al., 2012) and often higher reproductive success (King et al., 2013; Wilson et al., 2010) (see Table 1).

It is important to note that individuals can respond differently to the

Table 1

Summarize bibliography of Coping style in farmed fish.

Fish species	Test	Coping style	Reference
Brown trout (Salmo trutta)	Resident intruder test, hypoxia, confinement	Proactive fish show a stronger behavior responses to hypoxia.	(Brelín et al., 2005)
Brown trout (Salmo trutta)	Net restraining test, introduction of a pike (Esox Lucius), novel environment	Wild and sea-ranched offspring differ in coping styles. Wild trout showed a more pronounced stress behavior than sea-ranched. Different in their responses is due to genetic or epigenetic effects.	(Lepage et al., 2000)
Rainbow trout (Oncorhynchus mykiss)	Hypoxia test	High responsiveness (HR) and low responsiveness (LR) using selected strains of fish. HR showed a lower limit for reacting to hypoxic situations.	(Laursen et al., 2011)
Atlantic salmon (Salmo salar)	Hypoxia test	Reactive fish remained in hypoxia, higher cortisol level following acute stress compared the reactive fish that left the hypoxia.	(Vindas et al., 2017)
European sea bass (Dicentrarchus labrax)	Conditioned place preference/avoidance test.	Proactive fish were defined by a stronger preference to the social stimulus and present a lower physiological stress responses to aversive environment compared to reactive fish.	(Millot et al., 2014)
	Net restrain test,	Bolder individuals were less stress reactive. Less stress reactive learned faster. Also, bolder learned faster. There is a positive link between boldness and cognition.	
Sticklebacks (Gasterosteus aculeatus)	Cortisol release rate, boldness assays (novel environment-object test, predation test), learning trials.	Proactive have lower cortisol concentration and they learn faster. Fish reared under high density (Reactive coping style) were less aggressive, darker, less likely to take risks, more neophobic compared to those reared under low density (Proactive coping style).	(Bensky et al., 2017)
Nile Tilapia (Oreochromis niloticus)	Density-dependent	Proactive individuals display a faster feed intake recovery in a novel environment and less neophobia compared to reactive.	Champneys et al. (2018)
Nile Tilapia (Oreochromis niloticus)	Novel Environment, Novel object test,	Shy individuals are more able to deal	(Martins et al., 2011)
	Net restraining test		
Sea bream (Sparus aurata)	Risk-taking test,		Carbonara et al. (2019)

(continued on next page)

Table 1 (continued)

Fish species	Test	Coping style	Reference
	Hormonal concentrations, Swimming activity	with high density, while Bold to low density. Bold behavior (proactive coping style) is more adaptive to a balanced environment, whereas shy (reactive coping style) behavior is more adaptable. High responsiveness fish exhibit higher locomotor activity with an intruder compare to Low.	
Rainbow trout (Oncorhynchus mykiss)	Locomotor activity	Low cortisol production is connected to low locomotor behavior to stress and anorexia.	Overli et al. (2002)

same stressor. As such, experiences which some individuals are tolerant to may be harmful to others, which is symptomatic of differing coping styles and highlights a need for further application of fish welfare and stress reduction management (Huntingford and Adams, 2005). Barreto et al. (2011) demonstrated differential stress responsiveness to acclimatisation in Nile Tilapia (*Oreochromis niloticus*) following transfer to a novel social-isolation tank, including changes to ventilation rate and feeding resumption. The deliberate selection of desirable traits in farmed Salmonids, including improved growth performance, is believed to have caused a shift towards more proactive coping styles, with farmed stocks demonstrating more aggressive and bolder behaviours (Huntingford and Adams, 2005). These traits in combination with others such as enhanced metabolic rate and reduced brain size are indicative of domestication syndromes (Wilkins et al., 2014).

Emotional reactivity and coping styles of fish have only received attention in terms of animal welfare in recent years, and the link between laterality, emotional reactivity and copying styles is rarely studied in fishes. However, investigations into the use of laterality for the monitoring of these parameters in terrestrial domesticated and farm animals is already underway. One such study proposes the use of paw preference to assess emotional reactivity in domesticated cats, hypothesising that this could lead to improved feline welfare through better cat-owner relationships (Wells and McDowell, 2019). Additionally, Barnard et al. (2018) suggests the potential use of investigating laterality for welfare risk in kennel dogs, identifying paw laterality as a predictor of specific coping style behaviours. Left-pawedness was associated with stress behaviours, including frequent change of state and vocalisations, with right-pawedness related to active and inactive behaviours, such as moving and resting. Similar findings were identified in sheep, although no directional trends were identified, strongly lateralised lambs and dams experienced higher emotional stress than their non-lateralised conspecifics, demonstrated through increased pairing behaviours (Barnard et al., 2016). Conversely, higher levels of corticosterone, a key stress hormone, during domesticated chicks' embryonic development impairs lateralisation, with non-lateralised individuals demonstrating a higher reactivity to stress once hatched (Freire et al., 2006). In sharks, strongly lateralised individuals were more reactive to stress (Byrnes et al., 2016) but no relationship was identified in zebrafish (Fontana et al., 2019).

To summarise, there is clear evidence of copying style in fishes, which are well studied in the context of aquaculture, and while laterality is being used to assess copying styles across a range of mammals it has

received little attention in fishes. Clearly further research needs to determine if the relationship can be used to better optimise fish welfare in aquaculture and the ornamental fish industry.

3. Concluding remarks

Humans interact with fishes in a number of ways, most of which have welfare implications. There is a growing public sentiment in the importance of fish welfare, particularly in the context of human food sources, scientific animal experimentation and companion animals. Here we have illustrated that laterality plays a key role in the development and evolution of fish behaviour including social behaviour, foraging and predator avoidance (Bisazza and Brown, 2011a,b). It has emerged that laterality may be involved in a complex domestication syndrome which includes personality, stress reactivity, changes in cognition and brain size. Importantly, we highlight the growing evidence of emotions in fishes and associated coping styles and illustrate the role that laterality plays in these areas that are clearly of interest in the context of fish welfare. In many instances we illustrate that laterality may be a useful indicator of welfare status and that laterality and associated behaviour may be manipulated by shifting environmental conditions. This provides mechanisms for those rearing fish in captivity, whether it be for scientific experimentation, production of fish for the aquarium trade or aquaculture, to actively select for the development of key traits during ontogeny. Moreover, because laterality has a heritable component, it is may also be possible to shape behavioural traits via artificial selection. Indeed, we suspect that this may already be happening in species that have had a long history of being reared in captivity, such as salmonids. This review has also highlighted the fact that most of the research on laterality has occurred under laboratory conditions and there has been little effort to examine the impacts of laterality in mass production contexts such as aquaculture directly. This remains an obvious avenue for future research.

Consideration of fish welfare, through farming fish under more optimal conditions such as reduced density and superior nutrition, can optimise growth and lower mortality (Lorenzen et al., 2012) improve file quality and shelf life (Digre et al., 2017). Thus, attending to fish welfare is often viewed as a win-win situation since it both improves the lives of fishes in captivity while simultaneously making sound economic sense.

Declaration of Competing Interest

None.

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