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Psychological and social well-being of bony fishes in zoos and aquariums (II)

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Abstract: Research on the behaviour of animals in zoos has been conducted for decades, and observations have provided information that has improved the psychological and social well-being of animals. However, research on fishes in zoos and aquariums seems to be lacking. Here, we assess the current state of research on fishes in zoos and aquariums by surveying the peer-reviewed literature. Our assessment differs from previous surveys in that we examine the taxonomic classes Chondrichthyes (sharks and rays) and Osteichthyes (bony fishes) separately. Our survey finds that bony fishes have been drastically underrepresented in zoo journals, more drastically than chondrichthyans, revealing an urgent need for zoos and aquariums to conduct research on the behaviour of the bony fishes in their care to ensure a positive state of psychological and social well-being. We conclude that data-driven analyses of fish behaviour could aid in the development of evidence-based practices that enhance the well-being of bony fishes in zoos and aquariums, just as they already do for terrestrial animals.

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1. Introduction. Animals in human care are subjected to factors that may have an impact on their welfare, such as food availability, available space, population size, and environmental complexity. Animal welfare is defined by the Association of Zoos and Aquariums as "an animal's collective physical, mental, and emotional states over a period of time, and is measured on a continuum from good to poor" (AZA, 2020). Research on the behaviour of zoo animals to improve their mental and emotional states has been conducted for decades (Powell & Watters, 2017). This type of research on psychological and social well-being addresses what is now being called the 'feelings-based' aspect of welfare, to contrast it from a purely health- and medically-focused aspect of welfare (*sensu* Veasey, 2017). Such studies investigate, for example, how animals interact socially with other individuals (Anderson et al., 2016) and how environmental enrichment affects animal behaviour (Carlstead et al., 1991). The studies typically focus on terrestrial zoo animals. The goal of such research is not only to eliminate negative conditions and experiences, but to elicit positive experiences (Koene & Duncan, 2001; Boissy et al., 2007; Rose & Riley, 2019). Indeed, Veasey (2017) argued that animals could potentially experience better welfare in zoos than in the wild. In contrast, little research seems to have been conducted on the psychological and social well-being of fishes in zoos and aquariums. In an aquarium, a fish may encounter conditions that differ from a natural environment in several respects. Variation in these factors can have harmful negative effects or positive pleasurable effects on well-being (Fife-Cook & Franks, 2019). It is not clear how much research has addressed bony fishes as opposed to sharks and rays. Osteichthyes is a taxonomic class more closely related to tetrapods than it is to sharks and rays, which comprise a separate class altogether: Chondrichthyes.

Previous surveys have repeatedly shown that fishes in general (including both Osteichthyes and Chondrichthyes) are not well represented in zoo and aquarium research. Stoinski et al. (1998) surveyed 173 North American zoos and aquariums with a questionnaire. More institutions reported studying behaviour than any other topic, and 26.0% of them claimed to study 'fish' (a category that presumably included both bony fishes and sharks and rays), which was less than any other category except for amphibians and 'other'. (Invertebrates were not included as a group.) In Europe, Melfi (2009) extracted data from the database Species360 (called ISIS at that time) to assess the taxonomic distribution of research projects undertaken between 1998-2008 in institutions of the British and Irish Association of Zoos and Aquariums. She found that 89.1% (690/774) of the projects were undertaken on mammals and only 1.0% (8/774) projects were undertaken on the combined category 'fish, invertebrates, and amphibians'.

Literature surveys show that fishes are also poorly represented in peer-reviewed zoo and aquarium journals. Wemmer et al. (1997) analysed the articles published during the first 15 years of the journal *Zoo Biology*. Consistent with Stoinski et al. (1998), they found that more articles were published on behaviour than on any other topic. They also found that 73.4% of all articles focused on mammals, and only 2.5% of articles focused on what they called 'fish', which was again less than any other taxon other than amphibians. (Again, invertebrates were not included as a group.) Only 5.5% of all articles had an aquarium employee (rather than a zoo employee) as senior author. A later study analysed the first 25 years of articles published in *Zoo Biology* (Anderson et al., 2008) and found that not much had changed in the 10 years since the survey conducted by Wemmer et al. (1997). Behaviour was still the most popular research topic, and research on fishes had not

expanded at all. Mammals were the subjects of 74.8%, and fishes of only 2.2%, of articles. Fishes comprised fewer studies than any other taxon, other than invertebrates at 2.1%. Goulart et al. (2009) conducted a worldwide survey of zoo and wild animal welfare research by searching the bibliographic database Web of Science© for articles published between 1966-2007. Out of 1,125 abstracts on 236 different species, mammals were the most represented, being the subject of 75.9% of all studies. The search did not recover any studies at all on fishes. More recently, Binding et al. (2020) conducted a survey of peer-reviewed articles focusing on animal welfare research performed in zoos and aquariums published from 2008-2017. Again, mammals were the most studied group, being the subjects of 74.8% (232/310) of articles, and 'fish' were lowest, with only 0.6% (2/310) of articles, and behaviour was by far the most commonly used welfare parameter, with 81.0% of all articles focusing on behaviour. All these surveys used a category called 'fish', which presumably included both bony fishes and sharks and rays. Sharks and rays are popular aquarium animals, and many of the studies identified in these surveys as being conducted on 'fish' may have been conducted on sharks and rays and not on bony fishes. Thus, we thought it important to question how much zoo and aquarium research is actually conducted on sharks and rays and how much is conducted on bony fishes.

One recent literature survey published the raw data recovered in the search, including a summary of each article. Rose et al. (2019) extracted data ranging from 2009 to 2018 from the Web of Science©, and compared the number of zoo-related articles for each taxon to the mean number of species held in zoos worldwide, as reported in the *International Zoo Yearbook*. As found by previous surveys, more studies were performed on mammals than on any other taxon, but the greater availability of bird and fish species in zoos revealed that the attention given to mammals was even more biased than it had previously seemed. Of the mere nine studies recovered that somehow pertained to 'fish' in zoos, four pertained to sharks, and five pertained to bony fishes. However, several of those studies did not even involve animals that were actually in zoos or public aquariums.

Bony fishes are now recognized to be complex individuals of advanced cognitive ability (Balcombe, 2016). For the past 20 years, debate has raged on whether bony fishes have the ability to feel pain (Braithwaite, 2010), and the consensus now is that they can (Key, 2016; Woodruff, 2017). There is also evidence (reviewed by Kittilsen, 2013) that bony fishes feel fear and other emotions. Experiments have shown that bony fishes have cognitive capacities. In one study, the mosquitofish *Gambusia holbrooki* discriminated between shoals of conspecifics that differed in size by one individual when faced with choices of 1 vs. 2, 2 vs. 3, and 3 vs. 4, but not in a choice of 4 vs. 5 individuals, showing that at least one fish species has a rudimentary ability to 'count' to four (Agrillo et al., 2008). The African cichlid *Astatotilapia burtoni* is capable of transitive inference (Grosenick et al., 2007). This occurs when an individual can infer a relationship between two other individuals based on the relationships that each one has with a third party. Bony fish learn traditions from each other by socially transmitting information across generations (reviewed by Brown & Laland, 2003). Individuals of one species, the cleaner wrasse, *Labroides dimidiatus*, have recognized themselves in a mirror (Kohda et al., 2019), which in other vertebrates has been interpreted to indicate self-awareness (Plotnik et al., 2006). Using human psychology literature as a foundation, Galhardo and Oliveira (2009) argued that the detection of sensory inputs results in stimulus appraisal and the generation of mental representations in bony fishes. The question of whether bony fishes are self-aware might never be answered (Dawkins, 2017), but it seems that

they experience at least some degree of suffering and pleasure (Chandroo et al., 2004; Balcombe, 2009). Giving them the benefit of the doubt may motivate caregivers to think critically about the subjective experiences of suffering and pleasure in bony fishes held in human care (Birch, 2017).

In the current study, our goal is to elucidate how much research has been conducted on the psychological and social well-being of bony fishes in zoos and aquariums and identify future research that could fill any gaps in that area. To assess the history of research on bony fishes in zoos and aquariums, we conducted a literature survey that specifically considers bony fishes separately from sharks and rays. Next, we discuss the few studies that have been conducted on the behaviour of bony fishes in zoos and aquariums. To identify the types of studies that could be conducted in the future to ensure positive psychological and social well-being of bony fishes in zoos and aquariums, we draw examples from research conducted on bony fishes in other contexts, including commercial food-fish aquaculture and biomedical research. Finally, we present a vision for the future that would ultimately result in evidence-based husbandry practices (Melfi, 2009).

2. Surveying the taxonomic focus of articles published in zoo journals. To investigate the proportion of zoo- and aquarium-based research that is conducted on bony fishes compared to the other vertebrate classes, including class Chondrichthyes, the sharks and rays, we surveyed three zoo-oriented research journals: *Zoo Biology*, *Journal of Zoo and Aquarium Research*, and *International Zoo Yearbook*. We did not examine another prominent zoo-oriented journal, the *Journal of Zoo and Wildlife Medicine*, because of its focus on health and the medical aspects of welfare, and our study's focus on the feelings-based aspect of welfare. Neither did we include the public aquarium-oriented journal *Drum and Croaker*, as it is informal and not peer-reviewed. We also excluded *Aquarium Sciences and Conservation* (Burgess, 1997) because it had only three published volumes (1997-2001). To compare our findings with other disciplines, we surveyed two additional journals that publish on similar topics but do not focus on zoo animals: *Animal Behaviour* and *Conservation Biology*. Although Stoinski et al. (1998) found that zoos responding to their survey claimed to publish in *Animal Behaviour* and *Conservation Biology*, Hosey (1997) found that out of 163 papers published on captive vertebrates in *Animal Behaviour* from 1993-1994, only three involved animals in zoos. The vertebrate classes do not contain equal numbers of species, so it might be expected that more studies are published on more speciose classes. Whereas Melfi (2009) considered the differences in the number of individual animals of each species held in zoos, and Rose et al. (2019) considered the differences in the number of species in each class held in zoos, we chose to consider the differences in species richness across classes (for a similar approach see Rosenthal et al., 2017). To obtain the current number of valid species in each class, we consulted authoritative sources and recorded the values in Table 1.

We surveyed the articles published in the journals from January 2007 to January 2019. The *Journal of Zoo and Aquarium Research* began publication in 2013, so all existing articles were included. The number of articles focusing on species of each vertebrate class was quantified per journal. Only research articles and reviews were counted. Commentaries and other miscellaneous categories were not included. To assess the focal class of each article, the title and abstract were examined. For each journal, a Pearson Correlation between species richness and number of articles of each vertebrate class was calculated.

TABLE 1. Species richness by vertebrate class

Taxon	**# of Species**	**Source**
Mammals	6,495	https://mammaldiversity.org/ †
Birds	10,896	https://www.worldbirdnames.org/ †
Reptiles	10,793	http://www.reptile-database.org/db-info/SpeciesStat.html ‡
Amphibians	8,004	https://amphibiaweb.org/ ‡
Bony Fishes	33,449	http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp †
Cartilaginous Fishes	1,448	http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp †

† viewed 21 March 2019, ‡ viewed 8 April 2019

3. Correlation between number of articles and species richness. The numbers of articles published were not statistically correlated with the species richness of each class, for any of the journals analysed (Table 2).

TABLE 2. Pearson correlations between species richness across vertebrate classes and taxonomic distribution of articles in selected journals †

Journal	**r**	**Degrees of Freedom**	**p**
Zoo Biology	-0.2776	4	0.5943
J of Zoo and Aquarium Research	-0.2287	4	0.6629
International Zoo Yearbook	-0.2015	4	0.7018
Animal Behaviour	0.0308	4	0.9537
Conservation Biology	0.1100	4	0.8356

† Spearman rank correlations produced similar results

All three zoo journals overrepresented mammals, but only slightly underrepresented birds, and largely underrepresented reptiles, compared to the number of species in each class (Figure 1a). Amphibians were largely underrepresented in both *Zoo Biology* and *Journal of Zoo and Aquarium Research* but well represented in *International Zoo Yearbook*. Bony fishes were drastically underrepresented. They were represented most strongly in *International Zoo Yearbook*, which featured 5.2% (14/267) of articles on bony fishes, but that number was bolstered by one single special issue dedicated to freshwater fishes and their conservation (McGregor Reid, 2013). *Zoo Biology* had only 1.4% (9/639) of articles on bony fishes and only 2.3% (15/639) of articles on sharks and rays. *Journal of Zoo and Aquarium Research* had 4.2% (6/144) of articles on bony fishes and 3.5% (5/144) on

sharks and rays. Sharks and rays were completely absent from *International Zoo Yearbook*. In zoo journals overall, the number of studies on sharks and rays was similar to the number on bony fishes, but they were not underrepresented, owing to the lower number of extant species of sharks and rays compared to bony fishes: Osteichthyes is the most speciose vertebrate class, consisting of 33,449 species, whereas Chondrichthyes is the least speciose class with only 1,448 species (Fricke et al., 2019).

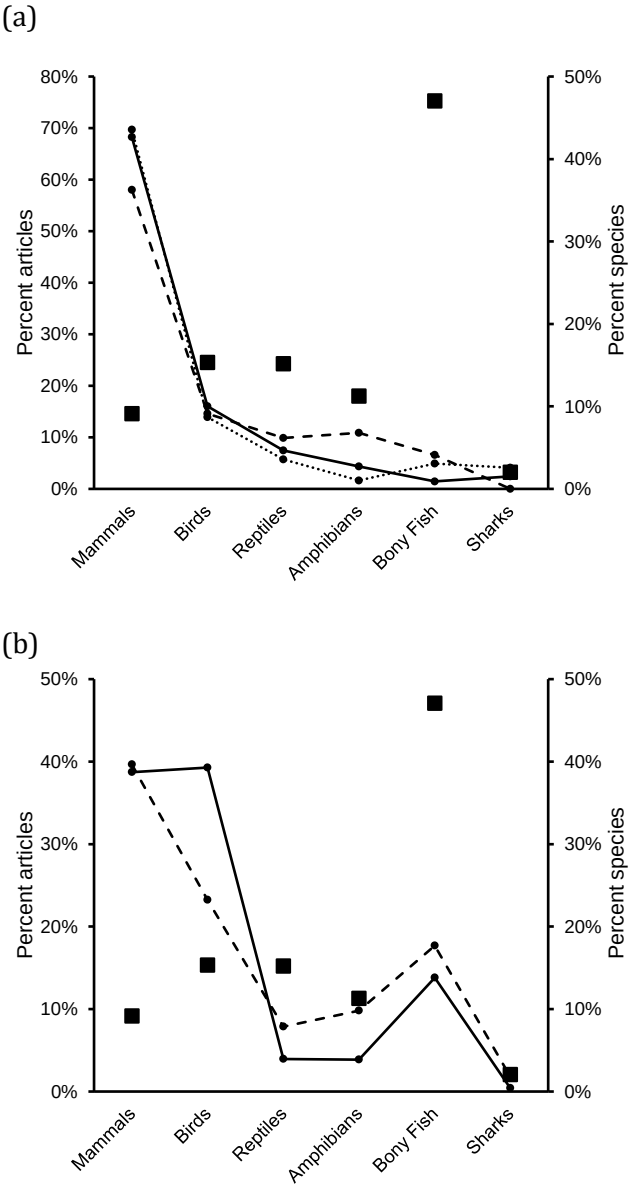

Figure 1. Research bias across vertebrate classes in both zoo- and non-zoo-oriented journals. (a) Percent of articles focused on each class in *Zoo Biology* (solid line), *Journal of Zoo and Aquarium Research* (dotted line), and *International Zoo Yearbook* (dashed line). (b) Percent articles focused on each class in *Animal Behaviour* (solid line) and *Conservation Biology* (dashed line). Black squares represent percent species per class extant across vertebrates based on data in Table 1. Chondrichthyes are represented as "sharks" on the graph for simplicity.

In the non-zoo journals, *Animal Behaviour* and *Conservation Biology*, a similar bias toward mammals was identified, but not to the extent seen in the zoo journals (Figure 1b). Unlike

in the zoo journals, birds were overrepresented in both *Animal Behaviour* and *Conservation Biology*. Reptiles were underrepresented in both journals. Amphibians were underrepresented in *Animal Behaviour*, but not in *Conservation Biology*. Bony fishes were underrepresented in both *Animal Behaviour* and *Conservation Biology*, but not to the extent that they were underrepresented in zoo journals. As in the zoo journals, sharks or rays were the subjects of very few articles, but they were not underrepresented according to their relatively small number of extant species.

A special issue of *Zoo Biology* dedicated to aquarium science included articles that focused on mammals, birds, reptiles, sharks, and corals, but not a single article focused on bony fishes (Goertmiller, 1993). Even research conducted at public aquariums focuses mostly on mammals, although fishes represent more than 50.0% of species held at aquariums (McCormick-Ray, 1993).

Of the few studies in zoo journals that focused on bony fishes, none of them addressed psychological and social well-being. In the special issue of *International Zoo Yearbook* dedicated to freshwater fishes and their conservation (McGregor Reid, 2013), out of 11 articles not one addressed psychological and social well-being. Articles were limited to topics such as disease (Routh, 2013) and general husbandry (Hemdal & McMullin, 2013).

4. State of the art and vision for the future.

4.1 Past taxonomic surveys not focused on zoos and aquariums. Bony fishes have been drastically underrepresented in zoo journals, revealing an urgent need for zoos and aquariums to conduct research on the behaviour of bony fishes to ensure a positive state of psychological and social well-being. Our literature survey found that mammals were overrepresented and bony fishes were underrepresented in zoo research. Surveys conducted outside the zoo community revealed a similar pattern, and like the zoo surveys, those studies neglected to assess sharks and rays separately from bony fishes.

Bautista & Pantoja (2005) examined 1,308,244 articles published between 1978-1998 and assessed the relationship between the number of articles and the number of species in each of 16 taxonomic groups and found that mammals were the most overrepresented, followed by birds, while fishes were the subject of proportionally less literature. Only the groups 'Insecta' and 'other arthropods' were less well represented based on the number of extant species. Fishes were also underrepresented in a literature survey on environmental enrichment across all contexts (Azevedo et al., 2007): In a search of the Web of Science across the years 1985-2004 that produced 744 abstracts that included farm animals and lab animals in addition to zoo animals, mammals were the most common taxonomic classification, making up 90.2% of all abstracts, the percentage of studies on fishes, at 0.4%, fell below birds, reptiles, and invertebrates, but not amphibians, which made up 0.0% of all abstracts.

The results of our survey were also consistent with the overrepresentation of mammals and birds that had previously been reported in *Animal Behaviour* by Rosenthal et al. (2017). Our results differed from theirs only in that we classified fishes as underrepresented whereas Rosenthal et al. classified fishes as overrepresented because they included invertebrates in their analysis. (Invertebrates were drastically underrepresented owing to the vast number of extant invertebrate species.) Our results indicate that across the biological sciences researchers tend to over-represent mammals and underrepresent fishes, but in zoo and aquarium research sharks and rays receive a proportionate amount of attention whereas bony fishes are particularly overlooked. Finally, the small amount of research conducted on bony fishes in zoos and aquariums

has typically focused on topics other than ensuring their psychological and social well-being.

4.2 Past studies of bony fish behaviour in zoos and aquariums. Some studies have examined behaviour of bony fishes in a zoo/aquarium context, and although these did not evaluate well-being, they nevertheless provide examples of how fish behaviour could be studied in zoos and aquariums. Probably the earliest study to systematically examine behaviour of fishes in public aquarium displays was done at the Suma Aquarium of Kobe City, Japan. Ryonosuke Okuno (1963) observed the behaviour of 52 species of marine fishes in the ocean, in a large aquarium, and in small aquariums, and noted striking differences in social behaviour when fishes were held in the smaller aquariums. Others around that time, e.g., Lorenz (1963), had remarked that fishes of many species behave more aggressively in aquariums than they do in the wild. However, Okuno was probably the first to recognize that the reduced space provided by small aquariums caused increases in aggression in fishes held in a zoo/public aquarium setting. Although his goal was to advance human understanding of social behaviour, his findings have obvious implications for the social and psychological well-being of fishes in zoos and aquariums.

Prappas et al. (1993) studied reproductive behaviour in the sergeant major, *Abudefduf saxatilis*, in The Living Seas Aquarium at Walt Disney World. Although their study was not intended to evaluate welfare, they found the spacing and reproductive behaviour of the fish to be consistent with that reported for wild fish, meaning that The Living Seas Aquarium had provided spatial conditions that allowed individuals to express their innate behaviour, which may have positive welfare implications. Kelley et al. (2006) compared the behaviour of butterfly splitfins, *Ameca splendens*, bred for 80 generations over 40 years at the London Zoo with the behaviours of wild fish in their native environment in Mexico and observed that wild fish spent more time searching for food. In a controlled experiment, they found that captive-bred fish performed more aggressive behaviour than wild-caught fish, and three-dimensional structure elicited less foraging behaviour and more aggressive behaviour than a bare environment. These studies did not set out to study psychological and social well-being, but they produced knowledge that might eventually be used to enhance it.

The first published study to intentionally assess the psychological and social well-being of a bony fish held in a zoo or public aquarium (Oldfield, 2011) compared the behaviour of Midas cichlids, *Amphilophus citrinellus*, in small glass aquariums, in a large exhibit at the Toledo Zoo, and in the wild. This species was extremely aggressive in small aquariums—which had obvious negative welfare effects in the form of injury and anxiety (cowering in the corner of the tank)—but not in the large zoo exhibit or in the wild. However, the fish in the zoo spent much less time foraging than the wild fish and instead spent most of their time hovering motionless. These animals were in excellent physical health, and they did not seem to suffer stressful social conditions. However, their enclosure failed to elicit the full range of positive behavioural experiences of which the species is capable, depriving them of the chance to express their innate capabilities and live a life as rich as possible (Nussbaum, 2006).

Burgess (2018) manipulated food placement in a display aquarium at the National Marine Aquarium in Plymouth, UK, and observed a decrease in aggression in regal tangs, *Paracanthurus hepatus*, and yellow tangs, *Zebrasoma flavescens*. As part of a PhD dissertation, Farmerie (2018) asked human participants to judge the welfare of koi,

Cyprinus carpio, at the Pittsburgh Zoo & PPG Aquarium. Participants felt that experiences with koi enhanced the health and well-being of both humans and koi.

Palagi et al. (2020) observed the African cichlid *Tropheus moorii* in an aquarium at the Natural History Museum of the University of Pisa, Italy, and found that aggression temporarily decreased and the social hierarchy changed when individuals of other species were added to and removed from the aquarium. They interpreted this to have implications for the animals' quality of life because dominance hierarchies are known to affect health, access to food, and reproductive potential.

Lawrence et al. (2021) compared the behaviour of two chondrichthyan and two bony fish species before and after an exhibit renovation at the Melbourne Zoo. After replacing crushed shell substrate with sand, adding shelters, and installing a barricade to keep visitors' hands out of the exhibit, they observed reduced stereotypic perimeter- and surface-swimming in four sharks, increased time spent resting in a stingray, and increased use of the exhibit space in two bony fishes.

4.3 How to study fish well-being in zoos and aquariums. Research on the psychological and social well-being of bony fishes is rapidly increasing in non-zoo contexts (Kristiansen et al., 2020). It began in Europe as a response to public concerns over the treatment of fishes in fish farming (Kristiansen & Bracke, 2020). It has since spread to include diverse human-fish interactions including commercial fishing, recreational fishing, ornamental fish trade, and biomedical research (reviewed by Huntingford et al., 2006; Branson, 2008; Kristiansen et al., 2020). This body of research provides examples of the types of studies that could be conducted in zoos and aquariums. The conditions of fishes in zoos and aquariums differ from those of farmed fishes (e.g., longer lifespans, less crowding, enriched enclosures), but an aquarium nevertheless alters the same environmental factors that farming does: food availability, available space, population density, and environmental complexity (reviewed by Martins et al., 2012; Sneddon et al., 2016).

Changes in feeding behaviour are well known indicators of welfare in bony fishes. Both latency to start feeding and daily food intake are often reduced as a result of stress from poor water quality or social conditions, or from netting and manipulation (Martins et al., 2012). Greater food consumption would seem to 'feel' better to a fish than lower food consumption (Balcombe, 2009). However, food consumption must be interpreted with caution. In some cases, reduced feeding is an adaptive response to positive experiences: In many cichlids, adults stop feeding when caring for offspring (e.g., Mrowka, 1984). On the other hand, subordinate individuals of the group-living goby, *Paragobiodon xanthosomus*, may intentionally forego eating to reduce their own growth rate and thus reduce competition with a dominant individual, showing that amount of food consumption can have varied motivations (Wong et al., 2008). Food limitations can lead to increases in aggressive interactions in both laboratory and fish farm contexts (Blackenhorn, 1992; Moutou et al., 1998). Aggression can have direct, immediate negative impact in the form of physical injury, which is typically assumed to induce pain and is generally interpreted as negative welfare (reviewed by Martins et al., 2012). A feeding regime that uses demand on the part of the animal, as is often done for terrestrial zoo animals (Regaiolli et al., 2020), has been provided for farmed fishes but this has not been done with zoo and aquarium fishes as far as we know (Almazán-Rueda et al., 2004; Noble et al., 2007). Quantitative behavioural observations would be an excellent way for zoos and aquariums to enhance their feeding regimes for individual bony fishes.

One of the most striking differences between an aquarium environment and a natural environment is the reduced amount of space available; it is hence possible that the reduced space might have a negative impact on well-being. The limited space available in an aquarium can prevent fishes from swimming. Depending on context and interpretation, locomotion can be a negative, stereotypic behaviour in zoo animals (Carlstead & Seidensticker, 1991), or it can be a positive experience (Marshall et al., 2016; Scott & LaDue, 2019). The same is true in food-fish aquaculture, in which locomotion has been interpreted either as poor welfare (Almazán-Rueda et al., 2004; Kristiansen & Fernö, 2007) or as positive welfare (Palstra & Planas, 2011).

In food-fish aquaculture, the number of individuals confined to a given space is calculated as stocking density. Both aquarium size and population size can independently affect fish behaviour; they interact as density, which may also affect behaviour. Tank size alone, even when population size and density are held constant, can affect fish social behaviour and well-being (Itzkowitz, 1977; Kristiansen et al., 2004). Population size may also affect well-being in bony fishes. Isolation may be appropriate for species that are solitary in nature (Seidensticker & Doherty, 1996), but other species require the presence of conspecifics to enhance their well-being (Coss & Globus, 1979; Blackenhorn, 1992; Brandão et al., 2015; Collymore et al., 2015). On the other hand, high density can negatively affect well-being in bony fishes (Burgess & Coss, 1982; Ramsay et al., 2006; van de Nieuwegiessen et al., 2008), often by stimulating aggression and increasing injury (Cañon Jones et al., 2011).

Quantitative analyses of behaviour could provide a valuable tool for zoos and aquariums to determine the optimal stocking densities for particular species in particular exhibit spaces. Social network analysis is a novel tool that provides more detailed information about the relationships among individuals in a group. Such analyses have been performed on farmed Atlantic salmon (Cañon Jones et al., 2011) and have been applied to better understand social relationships in animals in zoos (Rose & Croft, 2020). Formal analyses of social networks that provide measures of centrality, density, clustering coefficient, and distance have great potential to improve understanding of the social behaviour of bony fishes in zoos and aquariums (Krause et al., 2015).

One other striking difference between natural and aquarium environments is the reduced habitat heterogeneity experienced by the animals. The effects of environmental enrichment on bony fishes has been studied extensively in food-fish aquaculture and laboratory environments (reviewed by Näslund & Johnsson, 2016; Jones et al., 2021). Environmental enrichment has positive effects on brain development and cognitive ability (Kihslinger & Nevitt, 2006; Brown et al., 2003; Braithwaite & Salvanes, 2005) and reduces anxiety-like behaviours (Collymore et al., 2015). Environmental enrichment also has immediate effects when fishes interact directly with the material provided, reducing stress (Höglund et al., 2005) and permitting natural behaviour (Galhardo et al., 2008). Environmental enrichment often allows terrestrial zoo animals to seek out their own preferences (Melfi, 2009). In biomedical research too, bony fishes have been shown to prefer certain conditions over others (DePasquale et al., 2019). Physical structure also has immediate effects on their social behaviour, and often results in decreased aggression (Basquill & Grant, 1998; Barreto et al., 2011). Quantitative analyses of behaviour could be conducted on fishes in zoos and aquariums to determine how environmental enrichment may enhance psychological well-being.

4.3 Vision for the future. Why has the psychological and social well-being of fishes in zoos and aquariums been overlooked? The answer may lie in the history of the animal welfare movement (Powell & Watters, 2017). Understandably, the first concerns that humans had for animals in their care were simply to keep the animals alive and physically healthy (Melfi, 2009). The most pressing concern was to alleviate indicators of poor welfare. Additional welfare concerns arose in zoos because some mammals exhibited conspicuous behavioural aberrations (e.g., pacing), which motivated researchers to study the underlying causes so as to curtail their occurrence (e.g., Carlstead & Seidensticker, 1991). Three possible reasons that the psychological and social well-being of fishes in zoos and aquariums has been overlooked include: (1) Fishes were historically regarded as instinct-driven animals incapable of conscious thought (e.g., Key, 2016). (2) Aquarium researchers have been preoccupied with the chemistry and technology required to simply keep fishes alive in an aquatic environment (Goertmiller, 1993). (3) It may be more difficult for a human to identify with a fish and to recognize aberrant behaviour (Oldfield, 2022). Perhaps these reasons explain why the psychological and social well-being of fishes in zoos and aquariums is not as well understood as is that of mammals.

The future will see a shift from alleviating negative welfare to eliciting positive welfare in bony fishes (Fife-Cook & Franks, 2019). Data-driven analyses of behaviour could also help develop evidence-based practices to enhance the well-being of fishes in zoos and aquariums, just as they already do for terrestrial zoo animals (Watters et al., 2021). This view should not be interpreted as a condemnation of existing husbandry practices, but as a call to advance husbandry to the next logical step in its evolution (Powell & Watters, 2017). In the past, public aquariums have occasionally provided off-exhibit aquariums for research on bony fishes (Magnuson, 1962; Kallman, 1984; Vagelli & Volpedo, 2004; Dobberfuhl et al., 2005; Soares et al., 2017). Zoos and aquariums are in a position to publish studies in academic journals (Loh et al., 2018).

The psychological needs of animals include the freedom to roam, to forage, to hunt, to fight, to seek seclusion or the company of others, to take risks, and to make choices (Veasey, 2017). Based on what is now known about their cognitive abilities, there is no reason that these requirements would not apply to fishes just as they apply to other zoo animals. Moreover, fish welfare is important not only for ethical reasons, but also because continued human alteration of natural environments is going to make wild animals increasingly rare and captive animals ever more strongly regulated. It is inevitable that the public's demand to enhance animal welfare will spread from food-fish aquaculture and biomedical research to zoos and aquariums. Indeed, expansion of welfare concerns to all animal species will be a major next step in the evolution of human civilization. Research on fishes in zoos and aquariums has the potential not only to improve their welfare, but also to provide knowledge about species and behaviours that are otherwise inaccessible (Herrington et al., 2008; Oldfield et al., 2023). Ultimately, conserving the natural behaviour of an organism is a necessary part of conservation; without behaviour not all aspects of the organism are accounted for (Watters et al., 2003).

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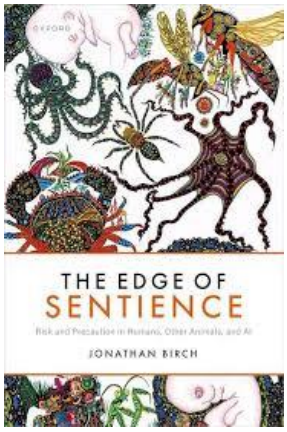
The Edge of Sentience:

Risk and Precaution in Humans, Other Animals, and AI

Jonathan Birch



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Abstract: Can octopuses feel pain and pleasure? What about crabs, shrimps, insects, or spiders? How do we tell whether a person unresponsive after severe brain injury might be suffering? When does a fetus in the womb start to have conscious experiences? Could there even be rudimentary feelings in miniature models of the human brain, grown from human stem cells? And what about AI? These are questions about the edge of sentience, and they are subject to enormous, disorienting uncertainty. The stakes are immense, and neglecting the risks can have terrible costs. We need to err on the side of caution, yet it's often far from clear what 'erring on the side of caution' should mean in practice. When are we going too far? When are we not doing enough? *The Edge of Sentience* presents a comprehensive precautionary framework designed to help us reach ethically sound, evidence-based decisions despite our uncertainty.

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