

Physical enrichment research for captive fish: Time to focus on the DETAILS

Nick A. R. Jones¹  | Mike M. Webster¹  | Anne Gro Veia Salvanes²

¹Centre for Biological Diversity, School of Biology, University of St Andrews, St Andrews, UK

²Department of Biological Sciences, University of Bergen, Bergen, Norway

Correspondence

Nick A. R. Jones, Centre for Biological Diversity, School of Biology, University of St Andrews, Sir Harold Mitchell Building, St Andrews, Fife KY16 9TH, UK.
Email: narj@st-andrews.ac.uk

Funding information

N.A.R.J. was supported by an FSBI studentship.

Abstract

Growing research effort has shown that physical enrichment (PE) can improve fish welfare and research validity. However, the inclusion of PE does not always result in positive effects and conflicting findings have highlighted the many nuances involved. Effects are known to depend on species and life stage tested, but effects may also vary with differences in the specific items used as enrichment between and within studies. Reporting fine-scale characteristics of items used as enrichment in studies may help to reveal these factors. We conducted a survey of PE-focused studies published in the last 5 years to examine the current state of methodological reporting. The survey results suggest that some aspects of enrichment are not adequately detailed. For example, the amount and dimensions of objects used as enrichment were frequently omitted. Similarly, the ecological relevance, or other justification, for enrichment items was frequently not made explicit. Focusing on ecologically relevant aspects of PE and increasing the level of detail reported in studies may benefit future work and we propose a framework with the acronym **DETAILS** (Dimensions, Ecological rationale, Timing of enrichment, Amount, Inputs, Lighting and Social environment). We outline the potential importance of each of the elements of this framework with the hope it may aid in the level of reporting and standardization across studies, ultimately aiding the search for more beneficial types of PE and the development of our understanding and ability to improve the welfare of captive fish and promote more biologically relevant behaviour.

KEYWORDS

environmental complexity, environmental enrichment, fish husbandry, fish welfare, structural complexity, structural enrichment

1 | INTRODUCTION

Fishes represent important laboratory animals, with increasing numbers of species used as model organisms in research (Braasch *et al.*, 2015; Laland *et al.*, 2011; Powers, 1989; Schartl, 2014; Utne-Palm & Smith, 2020). Increasing the diversity of model organisms can be a boon for research (Alfred & Baldwin, 2015) and fishes,

as the most numerous group of vertebrates, are of interest to many researchers. Fishes encompass a range of important ecological roles and specific niches with exceptionally diverse communities, for example in coral reef fishes (Stuart-Smith *et al.*, 2013) and rift lake cichlids (Muschick *et al.*, 2012), and represent a considerable diversity of morphology, behaviour and reproductive biology (Fernö *et al.*, 2020; Helfman *et al.*, 2009; Wootton & Smith, 2014). In addition to research

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Journal of Fish Biology* published by John Wiley & Sons Ltd on behalf of Fisheries Society of the British Isles.

opportunities, a large variety of species of fish is also kept in captivity for aquaculture and ornamental pets. When keeping animals in captivity, housing conditions play an important role in the welfare of captive animals and environmental enrichment is an important component of these conditions (Mason, 2010; Newberry, 1995; Shepherdson *et al.*, 1999; Swaisgood, 2007). However, relatively little is known about what enrichment to provide for most fishes in captive settings or the effectiveness of the different kinds of enrichment available. Comparatively few studies on the effects of enrichment have been conducted on fish, with an analysis of the literature in 2007 revealing that fish were subjects in less than 0.5% of all enrichment studies conducted on vertebrates (de Azevedo *et al.*, 2007). Of those studies involving fish, most are focused on relatively few species, with a focus on salmonids and zebrafish, *Danio rerio* (Hamilton 1822) (Näslund & Johnsson, 2014). This relative lack of knowledge is increasingly important to address as there is a mounting drive to improve and regulate welfare for fish species kept in captivity for research, aquaculture or ornamental reasons (Browman *et al.*, 2018; Jacobs *et al.*, 2018; King, 2019; Saraiva *et al.*, 2019; Sloman *et al.*, 2019; Sneddon *et al.*, 2017; Stevens *et al.*, 2017).

Physical enrichment (PE), also referred to as structural enrichment, is a form of environmental enrichment that generally refers to any form physical complexity added to housing for captive animals. Physical structure has long been known to provide potential benefits for fish and a heterogeneous environment can provide shelter from water currents, reduce aggression from other fish and act as landmarks around which to establish territories (Kalleberg, 1958). Knowledge of the importance and potential positive effects of PE has increased as research interest and effort has grown. It is now understood that adding PE to fish housing can have significant effects and may provide a range of potential benefits, both in terms of welfare for the fish, but also for research validity, where different housing and rearing environments can result in behavioural differences across studies involving the same species (Webster & Rutz, 2020). Experiments on effect of enrichment can also be relevant for the aquaculture industry as some studies of common aquaculture species have highlighted positive effects of enrichment. For example, PE has been shown to result in lower levels of cortisol in captive Atlantic salmon, *Salmo salar* (L. 1758), and Chinook Salmon, *Oncorhynchus tshawytscha* (Walbaum, 1792) (Cogliati *et al.*, 2019b; Näslund *et al.*, 2013; Rosengren *et al.*, 2016), and is a commonly ascribed tool to reduce stress in captive fish and improve welfare (Sneddon *et al.*, 2016; Stevens *et al.*, 2017). When discussing potential benefits of PE, we need to be clear what the beneficial outcomes can be for the fish in terms of welfare, better health, more stimulating environment, and also for scientists and aquaculturists where benefits may include improved survival and more 'natural' behaviour and physiological responses. Whether or not PE provides any benefit also depends on what that benefit is, how the 'benefit' is being valued and its connection to the goals of the enrichment programme. For example, a detailed study of the effect of PE on Atlantic salmon, *S. salar*, showed a welfare benefit for the fish from PE with reduced levels of cortisol and stress from disturbance, while mean growth was lower than in

unenriched tanks (Rosengren *et al.*, 2016). Decisions as to what PE to add to housing for fish must also take into account the pragmatic consideration of the need for usability and ease of maintenance (Lidster *et al.*, 2017). Research into the effects of PE is the primary way to inform these decisions.

There is a host of potential benefits afforded by enriched environments. Shelter provided by PE can reduce metabolic costs (Chrétien *et al.*, 2021; Finstad *et al.*, 2007; Millidine *et al.*, 2006). This, in conjunction with reduced levels of stress, may result in improved growth rates observed in *Oncorhynchus mykiss* (Walbaum, 1792) (Voorhees *et al.*, 2020; White *et al.*, 2019) and other species provided with shelter (Batzina & Karakatsouli, 2012; Zhang, Bai, *et al.*, 2019). The presence of PE can result in less physical damage to fishes, for example less dorsal fin damage was observed in structurally enriched tanks (Berejikian, 2011), and reduce the frequency of potentially damaging escape-related behaviours (Zimmermann *et al.*, 2012). Provision of PE may even increase survival in disease epidemics, for example juvenile *S. salar* reared in enriched environments showed greater survival in an outbreak of fish pathogen [*Flavobacterium columnare* (Davis 1922)] than fish raised in standard hatchery conditions (Räihä *et al.*, 2019). A physically enriched environment can also promote the development and expression of more varied and more ecologically relevant behaviours (Braithwaite & Bergendahl, 2020; Brown *et al.*, 2003; Sundström & Johnsson, 2001; Ullah *et al.*, 2017), affect brain physiology and development (Arechavala-Lopez *et al.*, 2020; DePasquale *et al.*, 2016; Fong *et al.*, 2019; Mes *et al.*, 2019; Salvanes *et al.*, 2013; Ullah *et al.*, 2020), and promote learning and performance in cognitive tests (Carbia & Brown, 2019; Roy & Bhat, 2016; Salvanes *et al.*, 2013; Strand *et al.*, 2010). Such positive effects of PE can result in improved survival in programmes where fish are raised in captivity for eventual release into the wild (Hyvärinen & Rodewald, 2013; Johnsson *et al.*, 2014; Lorenzen *et al.*, 2010; Mes *et al.*, 2019; Salvanes & Braithwaite, 2006). However, enrichment is not always found to increase post-release survival (Brockmark *et al.*, 2007; Solas *et al.*, 2019; Tatara *et al.*, 2009). Moreover, as Näslund and Johnsson (2014) pointed out in a comprehensive review of PE there are many nuances that can impact the effects of PE on fish behaviour and welfare. The presence of PE is not always beneficial. While some studies showed improved cognition and brain growth in fish kept in structured environments, other studies found no effect (Brydges & Braithwaite, 2009; Näslund *et al.*, 2019; Toli *et al.*, 2017) or even negative effects (Burns *et al.*, 2009) of exposure to PE. Similarly, despite zebrafish (*D. rerio*) displaying preferences for PE in choice tests (DePasquale *et al.*, 2019; Schroeder *et al.*, 2014), heavily enriched aquaria can lead to increased aggression and lower growth in the same species (Woodward *et al.*, 2019). Despite these many examples of positive effects found in studies of enrichment, knowledge gaps remain, highlighted by contradictory findings. There is limited knowledge on the types of enrichment that have effects and how they work (e.g., physiological and neurological processes). The general level of understanding might be summarized as some PE is better than none, some of the time.

What are the proximate reasons for fish to benefit from physical structure in captivity? In the most general sense structure can provide

shelter and protection from the physical environment and protection against other animals. The availability of shelter may be enough to provide benefits. One study showed that Atlantic salmon rested outside of shelters and suggested that the mere presence of a shelter was enough to significantly reduce metabolic rates (Millidine *et al.*, 2006). There are many studies that show that fish use structure as a form of antipredator refuge, and this may be the ultimate driver for use of and benefit from structure where protection from currents was secondary to protection from predators (Valdimarsson & Metcalfe, 1998). PE may afford refuge from many other things, including artificial lighting (McCartt *et al.*, 1997), intraspecific competition and aggression. Physical heterogeneity can potentially reduce aggression in territoriality species by, as in the rose bitterling *Rhodeus ocellatus* (Kner, 1866), affording landmarks that can be used to delineate territories, leading to reduced aggression between rival individuals (Smith, 2011). Similarly, individuals within a population can show specific characteristics which can lead to individual differences in shelter use. For example, in the wild older (and larger) female sockeye salmon, *Oncorhynchus nerka* (Walbaum, 1792), were shown to prefer and utilize deep-water refuges (Camacho & Hendry, 2020) while fish of other ages and sex clustered in different depths. These differences were attributed to the fact that larger females are more vulnerable to predation from bears when they return to spawn. Knowing the function of shelter use for a given species could allow researchers to select the optimum types of PE.

Despite the potential importance of PE, a survey of articles published in fish biology-focused journals (between 2003 and 2013) suggested that more than 70% of studies did not use any PE (Näslund & Johnsson, 2014). This is no doubt partly driven by one of the major challenges of using PE: adding PE to a tank can increase the difficulty of and time required for cleaning. A recent survey of husbandry practices in research laboratories highlighted this issue, with more than 60% of survey respondents considering provision of PE a challenge that required intensive labour and was thought to lead to an increased chance of disease (Lidster *et al.*, 2017). Developing forms of PE which can provide welfare benefits while reducing maintenance costs is an important challenge that will require further research into the various factors that can impact the costs and benefits of PE. It will also require the improvement of the standardization and reproducibility of studies exploring enrichment.

1.1 | Aims and scope

In this article we look at the current state of the research into PE, focusing on the specific forms of enrichment provided in studies. We conducted a survey of the recent literature to collate a representative selection of published articles and record the level of methodological detail currently reported. We point out issues that are commonly lacking when reporting results and make some recommendations for future work based on the survey results and recent publications which point towards potentially useful avenues of research for the field of enrichment. Our survey and review are focused on recent studies,

those published since 2015 when Näslund and Johnsson (2014) highlighted several important considerations for the field. Most pertinent to this article, they revealed that the effects of PE vary markedly across studies and suggested that future studies should attempt to differentiate more nuanced effects of different PE. The aim of our review is to extend this idea, specifically highlighting the need to understand what and why specific items of PE are used in studies. We provide a framework which we hope will help to guide researchers to consider and report more of the characteristics of the enrichment they use. We think more refined reporting, resulting ease of attaining higher levels of standardization and a deeper understanding of what PE to use at fine-scale levels will address the issues raised by Näslund and Johnsson (2014) and other authors (Huntingford *et al.*, 2006; Toni *et al.*, 2019).

2 | SURVEY APPROACH

To examine the current status of PE research in fish biology and the levels of reporting of PE details, we conducted a nonexhaustive survey of published research articles where PE was the focus or an important part of the aim of the study. In line with our aims this survey was used to collect a representative sample of papers currently published in the field rather than to conduct a formal meta-analysis. To do this one author (NJ) used Web of Knowledge to search for all papers with the terms 'physical enrichment' and/or 'structural enrichment' and/or 'environmental enrichment' and 'fish' from 2015 to May 2020. The resulting research papers that described experiments which included investigation of the effect of PE on captive fish were selected and included in the survey. For each paper, the introduction and methods sections were checked for the methodological details they reported, focusing on the description of PE used. We chose to collect data from the last 5 years to get a snapshot of the more recent PE-focused work and further the comprehensive review by Näslund & Johnsson (2014) which highlighted the importance of and nuances that can impact the effects of PE on captive fishes.

For each study we recorded the category of PE reported, for example whether a particular item of PE was a substrate or shelter, then recorded the general type of PE where an item of PE belonging to a substrate category could be gravel, sand or mud. For each type of PE, we recorded whether additional details were provided, such as the manufacturer and name of plastic plants, species name of live plants or some description of the shelter provided (*e.g.*, clay pot or PVC pipe). For each of these specific types of PE we recorded whether the specifications of those PE items were provided, for example the grain size and colour of gravel, length and diameter of PVC pipe, or the number, colour and size of leaves on plastic plants. We also recorded the amount of these PE items, for example numbers of plants added to the aquarium or the depth of gravel substrate. In addition, we recorded whether the rationale for the use of the PE was explicitly stated, essentially whether the PE used was chosen based on previous studies or in an attempt to mimic certain, normally wild, conditions.

TABLE 1 Data recorded during the literature survey

PE category	Type/rationale	Details	Amount/dimensions	Duration	Water parameters	Photo-period/lighting details	Fish density/ ^a parasite check	Species	Stage/origin	Study
Plants	Plastic/No	Green and red Hairgrass, Petco Animal Supplies, San Diego, CA	Yes/Yes	21	° C, conductivity, pH, alkalinity, ammonia, nitrite, nitrate	14:10 L:D/ No	No/Yes	<i>D. rerio</i>	A/CB	Collymore et al., 2015
Substrate	Gravel/Yes	No	Yes/Yes	V	No (natural source flow-through)	0:24 L:D/ Dark	No/No	<i>S. salar</i>	L/H	Evans et al., 2015
Shelter	In-tank structure/No	Plastic bricks	Yes/No	14	No	No/No	No/No	<i>O. fasciatus</i>	J/H	Makino et al., 2015
Shelter	In-tank structure/No	PVC pipes	Yes/No							
Plants	Plastic/No	Mock seagrass, Tanaka Sanjiro	Yes/Yes							
Substrate	Sand/No	No	No/No	V	° C, pH	12:12 L:D/ No	No/No	<i>D. rerio</i>	M/CB	Manuel et al., 2015
Plants	Plastic	No	No/No							
Shelter	In-tank structure	Artificial rock formation	No/No							
Substrate	Gravel/No	Fine grain	No/No	V	° C	12:12 L:D/ No	Yes/No	<i>O. mykiss</i>	J/H	Bergendahl et al., 2016
Shelter	In-tank structure/No	Black plastic pots	Yes/Yes							
Plants	Plastic/No	No	Yes/Yes							
Other	Novel objects/No	Ping-pong balls, green bottle tops, grey PVC pipes	No/No							
Shelter	In-tank structure/No	PVC pipes	Yes/Yes	60	° C, dissolved oxygen, pH, nitrite, nitrate, ammonia	12:12 L:D/ No	Yes/No	<i>C. gariepinus</i>	J/H	Boerrigter et al., 2016
Plants	Plastic/No	No	Yes/No	78	° C	12:12 L:D/ No	No/No	<i>D. rerio</i>	J/CB	DePasquale et al., 2016
Shelter	In-tank structure/No	Plastic shelter	No/No							
Substrate	Gravel/No	No	No/No							
Other	Novel objects/Yes	No	No/No							
Substrate	Gravel/No	No	No/No	15	° C, pH, dissolved oxygen, hardness, alkalinity, ammonia	14:10 L:D/ No	No/No	<i>D. rerio</i>	A/CB	Giacomini et al., 2016
Substrate	Sand/No	No	No/No							
Shelter	In-tank structure/No	Caps	No/No							
Plants	Live/No	Cabombaceae and Pontederiaceae	Yes/No							

TABLE 1 (Continued)

PE category	Type/rationale	Details	Amount/dimensions	Duration	Water parameters	Photo-period/lighting details	Fish density/ ^a parasite check	Species	Stage/origin	Study
Substrate	Sand/Partial	Smooth yellow sand	No/Partial	V	°C, pH, ammonia, nitrite, nitrate	12:12 L:D/ No	No/No	<i>R. clavata</i>	J/CB	Greenway et al., 2016
Substrate	Gravel/Partial	Course gravel	No/No							
Substrate	Plastic bottom/No	Grey plastic	No/No							
Substrate	Sand/No	Black	No/No							
Substrate	Sand/No	White	No/No							
Plants	Live/Partial	Algae (<i>Ascophyllum nodosum</i> , <i>Fucus vesiculosus</i>)	No/No							
Shelter	In-tank structure/Yes	Artificial refuge (bricks with a plastic lid)	No/No							
Shelter	In-tank structure/Yes	Vertically oriented round aluminium rods	Yes/Yes	51	°C, pH, dissolved oxygen, hardness, alkalinity, dissolved solids	No/No	Yes/No	<i>O. mykiss</i>	J/H	Kientz & Barnes, 2016
Other	Water movement/Yes	Controlled water velocities in the tank	NA/Yes							
Substrate	Gravel/No	No	No/No	V	°C	14:10 L:D/ No	Yes/No	<i>O. mykiss</i>	J/H	Pounder et al., 2016
Plants	Plastic/No	No	No/No							
Shelter	External shelter/No	Overhead cover	No/No							
Shelter	In-tank structure/Yes	Artificial refuge (shredded black polyethylene)	Yes/Yes	231	°C, dissolved oxygen	Natural light/ NA	Yes/No	<i>S. salar</i>	J/CB (F1)	Rosengren et al., 2016
Shelter	In-tank structure/Yes	Eucalyptus tree logs	Yes/No	60	No	Natural light/ NA	Yes/No	<i>P. lineatus</i>	J/H	Saraiva & Pompeu, 2016
Plants	Plastic/No	Artificial macrophytes; plastic bags cut into strips	Yes/No					<i>B. orbignyanus</i>		
Plants	Live/Yes	<i>Bacopa</i> sp. and <i>Ambulia</i> sp.	Yes/No	<1	°C, pH, ammonia, nitrite, nitrate	Natural light/ NA	NA/Yes	<i>C. auratus</i>	J/CB	Sullivan et al., 2016
Plants	Plastic/Yes	Model <i>Bacopa</i> and <i>Ambulia</i>	Yes/Partial							
Substrate	Sand/No	Coarse white sand	Yes/Yes							
Plants	Plastic/No	Plastic <i>Hygrophilja</i> leaves	Yes/Yes	V	°C, pH, conductivity, alkalinity, nitrate, nitrite.	12:12 L:D/ No	Yes/No	<i>D. rerio</i>	J/CB	Wafer et al., 2016
Plants	Plastic/No	Plastic grass	Yes/Yes							
Plants	Plastic/No	Grey with floating strands	Yes/Yes	60	°C	12:12 L:D/ No	No/No	<i>O. mykiss</i>	J/H	Bergendahl et al., 2017
Shelter	In-tank structure/No	PVC pipes	Yes/Yes							
Other	Novel objects/Yes	Weekly presentation of objects (e.g., a ball, plants, bottle lid)	No/No							

(Continues)

TABLE 1 (Continued)

PE category	Type/rationale	Details	Amount/dimensions	Duration	Water parameters	Photo-period/lighting details	Fish density/ ^a parasite check	Species	Stage/origin	Study
Shelter	In-tank structure/No	Plastic tube	Yes/Yes	3	°C, dissolved oxygen, pH, nitrite, nitrate, ammonia	12:12 L:D/ No	No/No	<i>A. egassizii</i>	A/WC	Kochham & Val, 2017
Substrate	Pebbles/No	No	No/No	70	°C	24:0L:D (constant)/ No	Yes/No	<i>G. aculeatus</i>	M/CB (F1)	Toli et al., 2017
Plants	Plastic/No	No	No/No							
Shelter	In-tank structure/No	Plastic cylinder	Yes/Yes							
Substrate	Gravel/No	No	Yes/Yes	120	No (natural source flow through)	No/No	No/No	<i>Tor putitora</i>	J/H	Ullah et al., 2017
Plants	Plastic	No	Yes/Yes							
Shelter	In-tank structure/No	PVC tubes	Yes/Yes							
Substrate	Sand/No	No	No/No	180	°C, salinity	16:8 L:D/No	No/No	<i>G. aculeatus</i>	M/CB (F1)	Abbey-Lee et al., 2018
Plants	Plastic/No	No	Yes/No							
Other	Novel objects/No	Variety	Yes/No							
Other	Sound/No	Music	No/Yes	15	°C, pH, dissolved oxygen, ammonia	14:10 L:D/ No	No/No	<i>D. rerio</i>	A/CB	Barcellos et al., 2018
Substrate	Image of gravel/No	No	No/No	63	°C, pH, conductivity, ammonia, nitrate, nitrite	12:12 L:D/ No	Yes/No	<i>D. rerio</i>	A/CB	Lee et al., 2018
Other	Movement to novel tanks/Yes	NA	NA/NA							
Substrate	Various/Yes	No	No/Yes	<1	°C, pH, ammonia, nitrite	No/No	Yes/No	<i>O. niloticus</i>	J/H	Maia & Volpato, 2018
Other	Thermal variability/Yes	Wide range (Tmin 9.6°C to Tmax 16.4°C) and restricted (Tmin 11.3°C to Tmax 12.7°C)	Yes/Yes	V	°C, dissolved oxygen, pH, nitrite, nitrate, ammonia	12:12 L:D/ No	Yes/No	<i>S. salar</i>	M/H	Sanhueza et al., 2018
Shelter	In-tank structure/Yes	Clay plot	Yes/Yes	17	°C	14:10 L:D/ No	Yes/No	<i>D. rerio</i>	A/CB	Sykes et al., 2018
Plants	Plastic/No	All Living Things Turtle Grass	Yes/No							
Substrate	Gravel/No	English sea stones (+ 'photo)	Yes/Yes		°C, pH, ammonia, nitrite, dissolved oxygen, alkalinity, hardness	14:10L:D/ No	Yes/No	<i>D. rerio</i>	A/CB	Marcon et al., 2018b
Plants	Plastic plants/No	'photo	Yes/Yes							
Shelter	In-tank shelter/No	Plastic 'ruin'	Yes/No							

TABLE 1 (Continued)

PE category	Type/rationale	Details	Amount/dimensions	Duration	Water parameters	Photo-period/lighting details	Fish density/ ^a parasite check	Species	Stage/origin	Study
Substrate	Gravel/No	English sea stones (+ 'photo)	Yes/Yes		°C, pH, ammonia, nitrite, dissolved oxygen, alkalinity, hardness	14:10 L:D/ No	Yes/No	<i>D. rerio</i>	A/CB	Marcon et al., 2018a
Plants	Plastic/No	'photo	Yes/Yes							
Shelter	In-tank shelter/No	Plastic 'ruin'	Yes/No							
Shelter	In-tank structure/No	Resin boat	No/No	183	°C, pH, dissolved oxygen	12:12 L:D/ No	No/No	<i>C. auratus</i>	J/NA	Abreu et al., 2019
Other	Water movement/Yes	No	No/No							
Plants	Live/No	No	No/No							
Shelter	In-tank structure/No	Plant-fibre ropes	Yes/No	35	°C, dissolved oxygen	10:14 L:D/ No	Yes/No	<i>S. aurata</i>	J/H	Arechavala-Lopez et al., 2019
Shelter	In-tank structure/No	Artificial log	Yes/Yes	300	°C, salinity	12:12 L:D/ No	Yes/No	<i>K. marmoratus</i>	M/CB	Berbel-Filho et al., 2019
Plants	Plastic/No	No	Yes/No							
Substrate	Sand/Yes	Fine sand	No/No	365	No	No/No	Yes/No	<i>B. coccosensis</i>	J/WC	Carbia & Brown, 2019
Plants	Live/Yes	Seagrass <i>Zostera muelleri</i>	No/No							
Shelter	In-tank structure/Yes	Formation with live oysters and shell fragments	No/No							
Substrate	Various/Yes	Shell grit with larger stones	No/No							
Other	Water movement/Yes	Tidal mimicking mechanism	Yes/Yes							
Shelter	In-tank structure/Yes	PVC (white) pipes bound together	Yes/Yes	200	°C	Natural light/ NA	Yes/No	<i>O. tshawytscha</i>	J/H	Cogliati et al., 2019
Substrate	Gravel/Yes	Resin embedded river rock	Yes/Yes							
Shelter	In-tank structure/Yes	PVC (white) pipes bound together	Yes/Yes	270	°C	Natural light/ NA	Yes/No	<i>O. tshawytscha</i>	J/H	Cogliati et al., 2019
Substrate	Gravel/Yes	Resin embedded river rock	Yes/Yes							
Shelter	In-tank structure/Yes	Vertically oriented round aluminium rods	Yes/Yes	127	°C, pH, dissolved oxygen, hardness, alkalinity, dissolved solids	No/No	Yes/No	<i>O. mykiss</i>	J/H	Crank et al., 2019
Other	Water movement/Yes	Controlled water velocities in the tank	NA/Yes							
Shelter	In-tank structure/No	Suspended coloured spheres	Yes/Partial							

(Continues)

TABLE 1 (Continued)

PE category	Type/rationale	Details	Amount/dimensions	Duration	Water parameters	Photo-period/lighting details	Fish density/ ^a parasite check	Species	Stage/origin	Study
Substrate	Sand/No	No	No/No	8	°C, pH, ammonia, nitrite, nitrate	12:12 L:D/ No	No/No	<i>D. rerio</i>	A/CB	DePasquale et al., 2019
Other	Water movement/Yes	Tidal mimicking mechanism	Yes/Yes							
Plants	Plastic/No	No	No/No							
Substrate	Gravel/Partial	Light-coloured	No/Yes	V	°C	12:12 L:D/ No	Yes/No	<i>P. reticulata</i>	A/CB	Fong et al., 2019
Plants	Live/No	Java moss (<i>Taxiphyllum</i> sp.)	Yes/Yes							
Other	Heterospecific/Partial	Water snails (<i>Planorbis</i> sp.)	Yes/No							
Other	In-tank structure/Partial	Artificial maze	NA/Yes							
Substrate	Gravel/No	No	No/No	<1	°C, pH, ammonia, nitrate	12:12 L:D/ No	Yes/No	<i>D. rerio</i>	A/CB	Jones et al., 2019
Shelter	External shelter/Yes	Overhead plastic cover	Yes/Yes					<i>G. aculeatus</i>	A/WC	
Plants	Plastic/Yes	No	Yes/Partial							
Substrate	Gravel/No	Aquarium gravel	Yes/Yes	V	°C, pH, conductivity, ammonia, nitrate, nitrite, filter flow rate	12:12 L:D/ No	Yes/Partial	<i>D. rerio</i>	M/CB	Lee et al., 2019
Plants	Live/Yes	Several species with sp. name	Yes/Yes							
Shelter	In-tank structure/Yes	Rocks	Yes/Yes	50	°C	Natural light/ NA	Yes/No	<i>S. salar</i>	J/H	Mes et al., 2019
Plants	Plastic/Partial	Eight black fronds	Yes/Yes							
Shelter	In-tank structure/Yes	Bundles of back polythene strips	Yes/Yes	231	°C, dissolved oxygen	Natural light/ NA	Yes/No	<i>S. salar</i>	J/CB (F1)	Näslund et al., 2019
Shelter	In-tank structure/No	Bricks	Yes/No	V	°C, dissolved oxygen, ammonia, salinity	No/No	Yes/Yes	<i>E. marginatus</i>	J/H	de Oliveira et al., 2019
Shelter	In-tank structure/Yes	Flat stones	Yes/No							
Shelter	In-tank structure/No	White PVC pipe	Yes/No							
Shelter	In-tank structure/No	Brown PVC pipe	Yes/No							
Substrate	Gravel/No	No	No/No	15	°C, dissolved oxygen	No/No	Yes/Partial	<i>S. salar</i>	J/H	Räihä et al., 2019
Shelter	In-tank structure/No	No	No/No					<i>S. trutta</i>	J/H	
Other	Water movement/No	Changes in flow direction	No/No							

TABLE 1 (Continued)

PE category	Type/rationale	Details	Amount/dimensions	Duration	Water parameters	Photo-period/lighting details	Fish density/parasite check	Species	Stage/origin	Study
Substrate	Gravel/Yes	Gravels of mixed shape and of greyish colour originated from a river Rhine, purchased from a materials trader. Quartz and flint splinters removed by hand.	Yes/Yes	V	°C, dissolved oxygen	No/No	Yes/No	<i>O. mykiss</i>	M/CB	Reiser et al., 2019
Shelter	In-tank structure/No	Plastic tube constructions	Yes/Yes	V	No	24:0L:D (constant)/No	No/No	<i>S. salar</i>	J/CB	Solas et al., 2019
Shelter	In-tank structure/Yes	Green box	Yes/Yes							
Shelter	In-tank structure/No	Bundles of wood	Yes/Yes	66	°C	No/No	Yes/No	<i>S. trutta</i>	JH	Watz, 2019
Shelter	In-tank structure/Yes	Vertically oriented round aluminium rods	Yes/Yes	V	°C, pH, dissolved oxygen, hardness, alkalinity, dissolved solids	No/No	Yes/No	<i>S. trutta</i> & <i>O. mykiss</i>	J/H	White et al., 2019
Shelter	In-tank structure/Yes	Vertically oriented round aluminium rods	Yes/Yes							
Shelter	In-tank structure/No	Upturned plant pot	Yes/Partial	63	°C	12:12 L:D/No	Yes/No	<i>D. rerio</i>	A/NA	Woodward et al., 2019
Plants	Plastic/No		Yes/No							
Shelter	External shelter/Yes	Opaque covering on one side of tank	No/No							
Plants	Live/No	Potted <i>Vallisneria spiralis</i> and <i>Echinodorus</i>	Yes/Partial	V	°C, pH, dissolved oxygen, conductivity	14:10 L:D/No	Yes/No	<i>S. notomelas</i>	A/WC	da Silva et al., 2020
Shelter	In-tank structure/No	Suspended balls of wool	Yes/No							
Shelter	In-tank structure/No	driftwood	Yes/Partial							
Shelter	In-tank structure/No	PVC pipe	Yes/Yes							
Shelter	In-tank structure/No	Tree branches	Yes/Partial							
Shelter	In-tank structure/No	PVC pipe	No/Yes	100	°C, pH, dissolved oxygen, ammonia, nitrite	12:12 L:D/No	Yes/No	<i>O. niloticus</i>	J/H	Favero Neto & Giaquinto, 2020
Plants	Plastic/No	Artificial water hyacinth	No/No							
Plants	Plastic/No	Red and green artificial plant	Yes/Partial	21	°C, conductivity, hardness, alkalinity, dissolved oxygen, ammonia, nitrate, and nitrite	14:10 L:D/Partial	Yes/Yes	<i>D. rerio</i>	A/NA	Krueger et al., 2020

(Continues)

TABLE 1 (Continued)

PE category	Type/rationale	Details	Amount/dimensions	Duration	Water parameters	Photo-period/lighting details	Fish density/ ^a parasite check	Species	Stage/origin	Study
Shelter	In-tank structure/No	Bricks	Yes/Yes	5	No	12:12 L:D/ No	Yes/No	<i>A. australis</i>	J/H	Rae et al., 2020
Plants	Plastic/Yes	Artificial seagrass	Yes/Yes							
Shelter	In-tank structure/Yes	Apparatus that mimicked floating algae	Yes/Yes	20	° C, pH, dissolved oxygen, ammonia, hardness, alkalinity	12:12 L:D/ No	Yes/No	<i>D. rerio</i>	A/NA	Soares et al., 2020
Substrate	Gravel/No	No	Yes/No	90	° C, dissolved oxygen, ammonia	12:12 L:D/ No	No/No	<i>T. putitora</i>	J/H	Ullah et al., 2020
Plants	Plastic/No	No	Yes/Partial							
Shelter	In-tank structure/No	PVC pipe	Yes/No							
Other	Novel objects/Yes	Plastic loops	Yes/Yes	<1	° C, pH, dissolved oxygen, ammonia, nitrate	No/No	V/No	<i>X. variatus</i>	A/CB	Vanderzwalm et al., 2020
Shelter	In-tank structure/Yes	Vertically oriented round aluminium rods	Yes/Yes	116	° C, pH, dissolved oxygen, hardness, alkalinity, dissolved solids	No/No	Yes/No	<i>O. mykiss</i>	J/H	Voorhees et al., 2020
Other	Water movement/Yes	Controlled water velocities in the tank	Yes/No							
Shelter	In-tank structure/Yes	Suspended plastic spheres	Yes/Yes							
Other	Water movement/Yes	Controlled water velocities	No/No	192	° C, oxygen, pH	12 h L:D/Yes	Yes/No	<i>C. macroponum</i>	J/NA	Pereira et al., 2020
Plants	Live plants/No	No	No/No							
Shelter	In-tank shelter/No	Resin boat	No/No							
Substrate	Gravel/No	No	No/No							
Substrate	Gravel/No	Multicoloured river stones/gravel	Yes/Yes	90	° C, oxygen, pH	12:12 L:D/ No	Yes/No	<i>C. idella</i>	J/H	Murtaza et al., 2020
Shelter	In-tank shelter/No	Cobbles	No/No							
Plants	Plastic/No	No	No/No							
Substrate	Stones/No	No	No/No	62	° C, oxygen, pH	No/No	Yes/No	<i>P. scalare</i>	J/CB	Diniz et al., 2020
Plants	NA/No	No	No/No							

TABLE 1 (Continued)

PE category	Type/rationale	Details	Amount/dimensions	Duration	Water parameters	Photo-period/lighting details	Fish density ^a /parasite check	Species	Stage/origin	Study
Substrate	Gravel/No	Pea gravel substrate	Yes/No		°C, ammonia, pH, nitrite, nitrate	12 h L:D/No	Yes/No	<i>P. reticulata</i>	A/CB	Masud et al., 2020
Shelter	In-tank shelter/No	Plastic tube	Yes/No							
Shelter	In-tank shelter/No	Flowerpot	Yes/No							
Plants	Plastic plants/No	Plastic reeds	No/No							
Plants	Plastic	No	Yes/No		°C, pH, ammonium, nitrite	14:10 L:D/No	Yes/No	<i>N. furzeri</i>	M/CB	Thoré et al., 2020
Shelter	In-tank shelter/No	Plastic T-shaped tubes	Yes/Yes							
Plants	Plastic/Yes	As used in previous studies	Yes/Yes	56	°C, dissolved oxygen, salinity, pH, ammonia, nitrite, and water flow	Natural/NA	Yes/No	<i>S. schlegelii</i>	J/H	Zhang et al., 2020
Plants	Plastic/Yes	Clear photo	No/Yes		°C, pH, conductivity		Yes/No	<i>D. rerio</i>	A/CB	dos Santos et al., 2020
Substrate	Stones/Yes	Clear photo	No/Yes							
Shelter	In-tank shelter/No	Plant-fibre ropes	Yes/No	60	°C, salinity, dissolved oxygen	12:12 L:D/No	Yes/No	<i>S. aurata</i>	J/H	Arechavala-Lopez et al., 2020
Substrate	Gravel/No	Grey-brownish gravel	Yes/Yes	V	°C	Natural/NA	Yes/No	<i>S. trutta</i>	M/H	Yaripour et al., 2020

Note. V, varied; NA, not applicable; for stage: J, juvenile; A, adult; L, larvae; M, multiple stages; for origin: CB, captive bred; H, hatchery bred; WC, wild caught. Duration is given in days unless specified otherwise.

^aIn some studies density is not reported and is included as no, but this may be due to fish being kept in isolation where density is not required.

In addition to the characteristics of each PE item reported we collected information on associated aspects of each study. We recorded the fish species tested and life stage exposed to PE and origin. We also recorded information regarding factors that are known to be or may also be important to consider in studies of the effects of PE, including whether the density of fish and the duration of the exposure to PE was reported for each study, photoperiod and lighting details, water quality parameters and evidence of whether or not pathogen checks were made.

3 | SURVEY RESULTS

3.1 | Reporting details of the PE used

Across the 65 studies surveyed we collected reporting details for 159 types of PE used (Table 1). Most studies reported some level of detail about the PE items used. In 68% of the cases either amounts or dimensions were reported. However, descriptions of both amounts and unit dimensions were reported in only 30% of occasions. Similarly, a rationale or justification for the use of specific types of PE was reported in less than half (39%) of the studies.

3.2 | At the study level

Of the species of fish tested in the studies, the majority (56%) were salmonids (30%) or zebrafish (26%). This reflects the major use of these fishes in aquaculture and research spheres and is similar to the level of research effort in studies published before 2015 (Näslund & Johnsson, 2014). Again, some potentially important details were frequently not recorded. For example, while most of the studies surveyed (79%) reported the photoperiod fish were kept in, only four of the 65 studies gave any further details of the lighting used.

4 | TOWARDS A MORE REFINED UNDERSTANDING OF PE

This survey of the literature revealed room for improvement in reporting details of PE provided for captive fish. Our results clearly demonstrate that in studies which investigate the effects of, or preferences for, PE there is often a lack of information on the details of the enrichment used. Using PVC pipes as an example, while commonly used as shelter for many fishes, the colour, size and diameter of the PVC pipes are not frequently considered in much detail. They are likely to be important, however, and a study with dusky grouper *Epinephelus marginatus* (Lowe, 1834) showed colour-biased preference between PVC tubes, favouring brown over white; potentially the fish preferred the lower colour contrast provided by the brown tubes (de Oliveira *et al.*, 2019). Lack of understanding of these elements may hinder the standardization of research methods and the ability to develop optimal housing and welfare for the fish species kept in

captivity. In this section we offer our approach to address this. First, we propose the DETAILS reporting framework to develop our understanding of specific characteristics of objects used as PE in studies and act as a guide for more standardized and nuanced reporting of PE. Second, in conjunction with this framework, we make recommendations that may help direct further research and help researchers determine the cues or characteristics of particular PE that fish respond to.

4.1 | The DETAILS reporting framework

Using selected examples, we can showcase the potential importance of reporting the aspects of PE where **DETAILS** (Dimensions, Ecological rationale, Timing of enrichment, Amount, Inputs, Lighting and Social environment) matter.

4.1.1 | Dimensions

What are the dimensions of shelter provided by the PE? What diameter of substrate grain do fish prefer or length of fronds of plants? Fine-scale characteristics of physical structures including the dimensions of shelter they afford is one important but frequently overlooked component and may help to account for studies which showed no effect of enrichment on behaviour or welfare. Two case studies are suggestive. The first is from a study of a small 'shell dweller' cichlid species from Lake Tanganyika, *Neolamprologus multifasciatus* (Boulenger, 1906), that uses empty shells to shelter from predators and also as brood chambers for their eggs. The cichlids show preferences for specific shell attributes, including size and level of intactness (Bose *et al.*, 2020). Similarly, sand gobies, *Pomatoschistus minutus* (Pallas, 1770), show preferences for certain sizes of clay pots that are used for nesting sites (Lehtonen & Wong, 2020). Certainly, grain size can be an important consideration when providing substrate, for example specific differences in gravel diameter were shown to affect the mortality of rainbow trout fingerlings (Reiser *et al.*, 2019). Fine-scale differences in dimensions between enrichment types may contribute to conflicting findings, for example where welfare benefits of PE are found in some but not all studies of zebrafish (Stevens *et al.*, 2021).

4.1.2 | Ecological rationale for the PE

The ecological and evolutionary factors underlying the observed preferences for and benefits of PE are not well studied, and where they are this is typically not explicitly part of the rationale used in many husbandry or welfare studies. However, this should be a fundamental aspect when selecting objects to use as PE. A recent study showcased the potential importance of ecology on use and preference for physical structures. A comparative study of 20 species of Lake Malawi cichlids showed that scores in standard behavioural assays, including

amount of time spent away from shelter in an 'open field test', were associated with the specific microhabitat that the species is commonly found in (Johnson *et al.*, 2020). Moreover, the authors suggest that the behavioural preferences may be linked to the microhabitats those species are associated with. Species which preferred edges or corners in experimental assays tend to favour narrow crevasses and caves characteristic of rocky habitats in the wild.

Substrate preferences are an area where ecological factors are relatively well known. The characteristics of the substrate used as PE for epibenthic species can be important, for example rays that actively bury themselves in substrates show strong preferences for substrates type, sand over gravel (Greenway *et al.*, 2016). The importance of substrate colour to reduce predation risk is also crucial where fish that match the colour of the background substrate are less likely to be predated (Browman & Marcotte, 1987; Ostrowski, 1989; Sumner, 1934). This has led to recommendations for salmonid aquaculture to acclimate fish raised in hatcheries to backgrounds with similar coloration to the gravel in the habitat where they will eventually be released (Donnelly & Whoriskey Jr, 1991). Besides colour, brightness of a substrate can also be important factor in fish preferences (Wu *et al.*, 2020), most likely for similar reasons. Substrate preferences can be driven by other aspects of an animal's ecology, for example three-spined sticklebacks, *Gasterosteus aculeatus* L. 1758, prefer complex substrates (with heterogeneous topography and colour) over simple substrates (homogeneously coloured and textured), but only when they are not satiated, suggesting preferences are linked to foraging preferences (Webster & Hart, 2004).

Many forms of PE that have welfare benefits may not have direct connection to the ecology of the fish, for example novel objects, behavioural engineering and stimulation. Water flow, or regulated changes in water flow, is one such form of enrichment that can promote exercise for fish with many associated benefits to welfare and growth (Huntingford & Kadri, 2013). Provision of water flow or other forms of enrichment which promote swimming and exercise will still benefit from considering ecological aspects, for example the maximum swimming and flow speeds may be based on natural water conditions.

4.1.3 | Timing of enrichment

There are three aspects of time which can affect whether or not PE has an impact or the size of the effect. First, the age or developmental stage of a fish can be particularly important. A recent study of the burrowing behaviour of the European eel, *Anguilla anguilla* (L. 1758), highlights the importance of understanding the different enrichment requirements across life stages, in this case substrate preference. Eels of different life stages showed preferences for different substrates in which to burrow: yellow eels preferred fine gravel (diameter 1–2 mm), with glass eels and elvers preferring coarse gravel (diameter 8–12 mm). They also showed different levels of use of burrows: glass eels showed greater urge to burrow than yellow eels (Steendam *et al.*, 2020). Similarly, Alnes *et al.* (in review) showed that Atlantic salmon at the fry life stage show no response to structural enrichment

stimuli but did so on reaching early parr stage 3 months later. The second aspect to consider is time of year or seasonality. Fish may use and benefit from PE at specific times in their lifecycle, but also at certain times of year, for example juvenile Atlantic salmon switch from being highly active, showing little usage of physical refuges, in summer to showing strong preference for antipredator refuges in winter (Valdimarsson & Metcalfe, 1998).

The duration of exposure to enrichment (or lack therefore) is the other synergistic aspect to consider when designing and reporting studies of enrichment. A study of rainbow trout, *O. mykiss*, showed that fish kept in enriched conditions for longer durations performed better in cognition assays (Bergendahl *et al.*, 2016). However, even short periods of exposure to PE can have effects as long as the fish were exposed to the enriched environments very recently prior to testing. For example, swimming agility and performance in behavioural assays improved even after relatively short exposure to enrichment (Bergendahl *et al.*, 2016, 2017; dos Santos *et al.*, 2020). Duration of studies can also be connected to social environment (discussed further below), where development of familiarity can lead to aggression as per Amazon mollies, *Poecilia formosa* (Girard, 1859) (Doran *et al.*, 2019), or reduce aggression in other species (Utne-Palm & Hart, 2000; Webster & Hart, 2006, 2007). Aggression can also increase at specific periods over the course of the development of hierarchies or changes in the reproductive cycles of fishes. For example, in the cooperatively breeding cichlid, *Neolamprologus pulcher* Trewavas & Poll, 1952, levels of aggression, and chemical signals that initiate or moderate aggression, have been shown to vary as a temporary response to changes in the hierarchy and social context (Bayani *et al.*, 2017; Wong & Balshine, 2011). Requirements and preferences for physical refuge are likely to depend on the reproductive stage and length of time within a tank in such systems.

4.1.4 | Amount

How much PE is needed to provide a welfare benefit? Knowing the percentage surface area to cover in shelter or volume estimates of substrate required per tank can help to create more efficient setups. Benefit should be maximized while keeping costs in terms of material and maintenance down. Until recently studies exploring PE in fishes have tended to focus on comparisons between enclosures with PE versus those that are completely barren, but the use and benefit of PE may depend on just how much of a particular type of enrichment is available. In the wild zebrafish have been observed in open water as frequently as amongst vegetation (Spence *et al.*, 2006) and having some unenriched space may be beneficial. For some species open unstructured areas might be more valuable than structure, and welfare can deteriorate with too much enrichment. For example, in captive sharptooth catfish, *Clarias gariepinus* Burchell, 1822, aggression (and resulting physical damage through biting) increased when tanks were provisioned with physical structure in the form of PVC tubes (Boerrigter *et al.*, 2016). Similarly, zebrafish kept in aquaria with 'medium' levels of enrichment performed better in welfare assays than fish from 'highly enriched' aquaria (Woodward *et al.*, 2019).

4.1.5 | Inputs

Inputs such as food and water are, of course, fundamental for maintaining fish in captivity. The physical and chemical properties of the water are also crucial, where water quality parameters such as dissolved oxygen and pH can impact stress and affect the underlying physiology, behaviour and ultimately welfare of fishes (Huntingford *et al.*, 2006; MacIntyre *et al.*, 2008; Stevens *et al.*, 2017; Williams *et al.*, 2009). Fishes exposed to even relatively short fluctuations in water quality in confinement showed behavioural changes with associated welfare implications (Vanderzwalmen *et al.*, 2021). As such, water quality parameters are frequently well reported in studies of enrichment, but not to the same level across studies. Differences in reporting of water quality likely reflect differences in fish species requirement but also enclosure type, for example studies using naturally fed flow-through tanks frequently report fewer water parameters. However, measuring and reporting the details of water chemistry are important in determining the effects or benefits of PE and affording more comparative or reproducible studies. Diet and differences in food types can also be important. Levels of dietary nitrogen can have impacts on welfare (Conceição *et al.*, 2012) and sources of nitrogen from specific diet formulations can affect growth and other welfare parameters (Bonaldo *et al.*, 2015). Live prey may be worth considering as a form of enrichment and can be fundamental to survival for many species (Ruyet *et al.*, 1993). Larval *Pseudochromis flavivertex* Rüppell, 1835, for example, do not survive without diets enriched with live prey (Olivotto *et al.*, 2006). The provision of live prey can be especially important for species reared in captivity for later release into the wild (Brown *et al.*, 2003).

Flow of water and current direction can in itself be a form of PE (DePasquale *et al.*, 2019), as can water changes (Lee *et al.*, 2018). Other environmental conditions can have subtle but important effects on fishes and may impact the findings of enrichment studies. For example, levels of turbidity can impact behaviour and level of social attraction and refuge use (Chamberlain & Ioannou, 2019; Fischer & Frommen, 2013). Temperature is an example of an easily measured and commonly included water parameter that has both direct and indirect effects on welfare. The provision of a varied thermal environment improved measures of welfare and growth in Atlantic salmon (Sanhueza *et al.*, 2018). Temperature can also impact preferences for physical complexity, for example minnows, *Phoxinus phoxinus* (L. 1758) significantly increased the time spent in refuges when the temperature dropped (Greenwood & Metcalfe, 1998). Temperature differences within a tank afforded by physical complexity in aquaria can impact use of particular areas or refuges for fishes exhibiting behavioural fever (Boltaña *et al.*, 2013; Huntingford *et al.*, 2020). Thermal preferences can also depend on the level of structural complexity or micro habitat, as shown for coral reef damselfish, *Chromis atripectoralis* Welander & Schultz, 1951 (Nay *et al.*, 2020). Various water parameters can also have interactive effects. For example, while high nitrate levels can reduce swimming speed and duration in juvenile silver perch, *Bidyanus bidyanu* (Mitchell, 1838), the effects can depend on or be masked by changes in temperature (Isaza *et al.*, 2020). Other environmental toxins can impact the preferred temperatures of fish (Petersen & Steffensen, 2003; Skandalis *et al.*, 2020).

Not all inputs are intentional, and parasites and other pathogens are an important welfare concern (Barber, 2007; Bui *et al.*, 2019). Pathogens can have many effects on fish, including effects on their behaviour and measures of welfare and potentially use of shelter (Gabagambi *et al.*, 2019; Martins *et al.*, 2012). They can also impact other measures of behaviour, for example parasites can impact cognitive performance (Barber *et al.*, 2017) and shoaling preferences. Three-spined sticklebacks, *G. aculeatus*, infected with the microsporidian, *Glugea anomala* (Moniez, 1887), for example, showed an increased shoaling tendency (Ward *et al.*, 2005).

4.1.6 | Lighting

Light, the intensity, wavelength and amount (photoperiod), is an important factor that is often overlooked in studies of PE. Light levels can have a large impact on fish behaviour, playing a crucial role in their behavioural ecology (Cerri, 1983; Keep *et al.*, 2020; McCartt *et al.*, 1997; Santon *et al.*, 2020), and can drive the use of shelter and shade. Light levels can impact levels of aggression (Valdimarsson & Metcalfe, 2001), which in turn can have significant impacts on fish welfare (da Silva *et al.*, 2020). Light can also impact growth (Boeuf & Le Bail, 1999). A study on blunt snout bream, *Megalobrama amblycephala* P. L. Yih, 1955, showed that high light intensity caused stress, elevated oxidative rate and immunosuppression, but low light intensity led to depressed growth, antioxidant capability and immunity (Tian *et al.*, 2015). Shade in aquaculture settings has also been shown to reduce levels of sea lice in pen-reared Atlantic salmon (Huse *et al.*, 1990).

Larval development and growth rates of zebrafish can be significantly impacted by light conditions (Villamizar *et al.*, 2014), and growth rate and aggression between individuals have been shown to improve with lower light intensity in other species too (Almazán-Rueda *et al.*, 2004; Arambam *et al.*, 2020; Boeuf & Le Bail, 1999; Rahman *et al.*, 2020; Tian *et al.*, 2015). Recent studies have focused on the effects of other aspects of light conditions on captive fish, such as the effects of acute bursts of light from photography (camera flash-light) (Knopf *et al.*, 2018), but despite the importance of light conditions, and the relationship with PE which may provide shelter and shade from lights, most studies exploring PE tend to ignore light and provide very few details outside of photoperiod.

4.1.7 | Social environment

Density of individuals in aquaria has long been known to impact behaviour (Ellis *et al.*, 2002), for example a recent study showed that killifish, *Nothobranchius furzeri* R. A. Jubbs, 1971, exhibit differences in body length, activity, aggressiveness and feeding behaviour across different densities (Thoré *et al.*, 2020). Beyond 'simple' fish density, social factors can impact the effects of or requirements for PE. Being a member of a group can provide many benefits (Ward & Webster, 2016), but most species of fish do not blindly form groups. Fish are able to differentiate between individuals and actively

moderate the composition of their groups (Ward *et al.*, 2020) and habitat complexity can, in turn, have a strong effect on social behaviour (Rodríguez-Pinto *et al.*, 2020). The benefit of social enrichment and preferred group sizes is species-specific (Saxby *et al.*, 2010) and can depend on the level of sociality of a species. Highly social species, obligate shoalers, can show strong preference for forming groups with conspecifics, for example zebrafish (Spence *et al.*, 2008), and can show well-developed discrimination between groups, preferring the larger group, for example *Lamprologus callipterus* Boulenger, 1906 (Durrer *et al.*, 2020). Specific aspects of social context, including group size, makeup and dynamics, can be important and may impact any observed 'benefit' of PE. Social context may even reduce the requirements for any PE at all. For example, solitarily housed zebrafish may use and gain benefits from structure (Collimore *et al.*, 2015), but in groups zebrafish showed no preference for PE (Jones *et al.*, 2019; Kistler *et al.*, 2011). Certain visual signs of activity of other fish can impact shoaling by zebrafish (Pritchard *et al.*, 2001) and large amounts of structure in a tank can lead to increased aggression in zebrafish (Woodward *et al.*, 2019) and other species (Boerrieger *et al.*, 2016).

Aggression is particularly important in captive environments, with effects on body condition and growth, and can be closely tied to social context. Levels of aggression between conspecifics can increase in captivity where movement is restricted (Doran *et al.*, 2019; Kelley *et al.*, 2006), especially in territorial species (Perrone *et al.*, 2019). Levels of aggression can depend on social dynamics, species composition, sex and stage of the individuals in a group (Bayani *et al.*, 2017; Desjardins *et al.*, 2012; McRobert *et al.*, 2012; Sloman *et al.*, 2011). While PE can reduce aggression by reducing line of sight between fishes or providing shelter from aggressors (Barley & Coleman, 2010; Torrezani *et al.*, 2013), this depends on the species involved and the amount of PE provided. Dominant individuals or species may use aggression to dominate shelter afforded by PE, for example when kept in aquaria together the threatened tilapia, *Oreochromis amphilas* (Hilgendorf, 1905), lose access to shelter to the more aggressive *O. niloticus* (Linnaeus, 1758) (Champneys *et al.*, 2020). Intraspecific aggression can increase with PE, as with butterfly splitfins, *Ameba splendens* R. R. Miller & Fitzsimons, 1971, but with no increased aggression towards heterospecifics (Jones & Magurran, 2014). It is also worth noting that PE can have more nuanced effects on social behaviour. A recent study on a *Serrapinnus notomelas* (Eigenmann, 1915) showed no effect of PE or density of fish on level of aggression but foraging rates went up with increasing enrichment and group size, with potential benefits for growth (da Silva *et al.*, 2020).

4.2 | Recommendations for future research

4.2.1 | Reporting DETAILS

Here we propose some simple examples of how and what authors might report for each aspect of the framework. The measures reported will depend on the type of enrichment used and the guidelines below (Table 2) are not exhaustive. Authors are encouraged to

add further relevant details given their specific species and experimental conditions as appropriate.

4.2.2 | Fine-scale characteristics of PE used by fishes

When providing PE that is intended to be used as shelter, what are the fine-scale characteristics of physical structures that fish respond to? Recent studies, as with the previously discussed preferences for specific colours of PVC pipes (de Oliveira *et al.*, 2019) or shelter dimensions (Bose *et al.*, 2020), suggest that aspects of physical structure can be important to fish seeking shelter, and fish may pay attention and respond to relatively subtle differences in shape, colour and contrast to the surrounds of the captive environment and sizes of shelter.

Further research into such nuances may also help to determine if there are general cross-species 'rules' that govern fish preferences for PE. Is there, for example, a relationship between body length and optimum refuge size across fish species that use a cavity-type shelter? If there are such general rules we should expect similar responses to enrichment in several species and this might allow for general guidelines for setting up captive environments for species that have not been studied directly.

4.2.3 | The importance of incorporating and comparing multiple types of PE

Frequently studies focus on comparing aquaria with some form(s) of PE to unenriched aquaria, but preferences of fish may depend on the available alternatives. Following the DETAILS framework may allow comparative studies and expose nuanced preferences. An example illustrating the importance of testing potential combinations of PE comes from an ecology-focused study on the Lake Tanganyikan cichlid, *N. pulcher*. The cichlids favoured more complex habitats (rocks with crevices) independent of whether or not sand substrate was available, but when rocks were not available the presence of substrate became important and they showed strong preference for sand (Josi *et al.*, 2018). Recent work has also shown that fish show preferences for specific combinations of PE. For example, zebrafish showed a preference for specific combinations of types of PE (plastic plants, in combination with sand substrate and directed water flow) over any one type of PE (DePasquale *et al.*, 2019, 2020).

4.3 | Grey literature

4.3.1 | PE repository: A call to share grey information

Given the major goal towards providing better welfare and reproducible science we think fish researchers should be encouraged to

TABLE 2 DETAILS reporting framework: Guidelines for what measures to report in studies using physical and structural enrichment

Dimensions	Substrate	Grain size (or range), specific colour hues. Perhaps some measure of mineral, or rock type.
	Plants	Natural (species) or artificial (manufacturer, model), average height, width of stem (especially for leafy stem species such as <i>Elodea</i>) and number of stems. For large leaved plants the average leaf size and number per stem.
	Other structure	Descriptive measurements, including size or volume of the whole object. Also, the number, position and dimensions of each of the openings/refuges. ^a
Ecological rationale ^b	Substrate	State the general relevance of substrate for study species, <i>i.e.</i> , benthic species or commonly associated with specific substrates. Is the substrate used in the study to mimic natural conditions for the species or for some specific reason(s)?
	Plants	Are the live plant species associated with the natural habitat of the species or do the live/plastic plants have similar physical characteristics and dimensions to habitat specific species? State the reason(s) for using the chosen plants.
	Other structure	State the reasoning for the use of the structure, relative to the goals of the study and ecology of the species. Explain why the number of items and their dimensions was selected.
Timing	Stage	Life history stage of species tested, and the season fish are collected and tested.
	Duration	Duration of time individual fish spend in both housing and experimental condition(s). Include the acclimation time prior to specific assays.
Amount	Substrate	Surface area covered within the tank and depth of sediment layer.
	Plants	Some indication of surface area of the tank covered by plants and/or the number of individual plants and density.
	Other structure	The number of items per tank would be a minimum to report but we would recommend including a ratio of shelters to fish number per tank.
Inputs	Chemistry	Water chemistry parameters and temperature as standard, but include some measure of variation over time, especially for fish housed for longer durations.
	Pathogens	Explicitly state whether checks for parasites or diseases were made.
	Flow	Some measure of water movement, <i>e.g.</i> , filter turnover rate.
Lighting	Photoperiod as standard, but include details of the lighting source, <i>e.g.</i> , manufacturer, wattage, hue, luminance and intensity.	
Social environment	Density of fish and sex ratio as standard, but also size (and size range) and relatedness. Include some measure of the level of sociality of the species, level of familiarity of fish housed and tested together, the social dynamics of the species, and how these may impact aggression and resource partitioning.	

^aFor individual items of physical shelter, *e.g.*, clay pots or tubes, dimensions should focus on the diameter of any openings fish may be expected to move through or rest within, but also the overall dimensions and size of the object, colour, and for less commonly used shelter types the texture of the material.

^bDecisions as to which objects to be provide as enrichment can be relatively simple when there is direct ecological relevance, *e.g.*, providing empty snail shells for shell-dwelling cichlids or plant species commonly found in the native habitat of the fish or artificial versions that mimic these plants. However, this information should be reported. Moreover, the specific details of particular items of enrichment may be informed by the ecology of the fish and help to connect with the details provided in other parts of the framework. For example, why are a set number of shelters used per tank, or per density of individuals? Why was one colour of substrate used?

publish or otherwise make public the enrichment requirements of their model species. In many cases research laboratories and professional aquarists have lots of experience with and good understanding of the PE requirements of their model species. We propose that scientists should be encouraged to publish this information to provide clear husbandry and PE requirements to act as guidelines for other researchers to use. While no doubt considered basic, low impact research, this can be fundamental to our understanding of the requirements of specific species and cross-laboratory standardization. We believe that scientists working with

a species in captivity would like to share their knowledge on fundamental information so that future generations of fish in captivity and researchers can build on existing knowledge. To that end we propose a publicly available repository, similar to that of Saraiva *et al.* (2019), but where information on environmental enrichment requirements and rationale for use of specific types of PE can be shared. Such a database would help to reduce the time and effort to find optimal husbandry setups when starting to work with a new species. It may also contribute to more standardized conditions across institutes and studies.

5 | SUMMARY

We highlight the need for developing more nuanced understanding of the factors that drive the use of PE and contribute to welfare improvements for captive fishes. There is a growing awareness and demand for more empirical studies and quantitative measurements of fish welfare (Brydges & Braithwaite, 2009; Huntingford, 2004; Huntingford *et al.*, 2006; Johnsson *et al.*, 2014; King, 2019; Näslund & Johnsson, 2014; Sloman *et al.*, 2019; Sneddon *et al.*, 2016; Turnbull & Huntingford, 2012). Answering fundamental questions around PE is a crucial aspect of that: knowing what type, how much and when to provide structure to maximize the benefits associated with PE will help to improve the welfare outcomes for fishes. The proposed DETAILS framework may help to achieve these goals by focusing researcher attention on these questions and providing a memorable guide to reporting of PE used across studies. In conjunction with recent preparatory guidelines (Smith *et al.*, 2018), our reporting framework may also benefit the reproducibility of empirical studies exploring the effects of enrichment. Ultimately, a more detailed knowledge of PE may allow the identification and implementation of design changes which can afford the benefits of PE while minimizing the costs associated with them, leading to benefits for the fish themselves and researchers, aquaculture industries and manufacturers of housing systems.

ACKNOWLEDGEMENTS

The authors would like to thank and dedicate this article to Victoria Braithwaite, whose work helped inspire this project. We would also like to thank the reviewers, whose comments greatly improved our manuscript. N.A.R.J. was supported by an FSBI studentship.

AUTHOR CONTRIBUTIONS

Nick A.R. Jones Conceived the original idea, conducted the survey, and wrote the first draft. Mike Webster and Anne Gro Veia Salvanes contributed conceptual ideas to the initial outline, draft manuscript, and revisions to the full manuscript.

ORCID

Nick A. R. Jones  <https://orcid.org/0000-0002-6031-7507>

Mike M. Webster  <https://orcid.org/0000-0001-9597-6871>

REFERENCES

- Abbey-Lee, R. N., Uhrig, E. J., Zidar, J., Favati, A., Almborg, J., Dahlbom, J., ... Løvlie, H. (2018). The influence of rearing on behavior, brain monoamines, and gene expression in three-spined sticklebacks. *Brain, Behavior and Evolution*, *91*, 201–213.
- Abreu, C. C., Fernandes, T. N., Henrique, E. P., Pereira, P. D. C., Marques, S. B., Herdeiro, S. L. S., ... Picanço-Diniz, C. W. (2019). Small-scale environmental enrichment and exercise enhance learning and spatial memory of *Carassius auratus*, and increase cell proliferation in the telencephalon: An exploratory study. *Brazilian Journal of Medical and Biological Research*, *52*, e8026.
- Alfred, J., & Baldwin, I. T. (2015). New opportunities at the wild frontier. *Elife*, *4*, e06956.
- Almazán-Rueda, P., Schrama, J. W., & Verreth, J. A. J. (2004). Behavioural responses under different feeding methods and light regimes of the African catfish (*Clarias gariepinus*) juveniles. *Aquaculture*, *231*, 347–359.
- Arambam, K., Singh, S. K., Biswas, P., Patel, A. B., Jena, A. K., & Pandey, P. K. (2020). Influence of light intensity and photoperiod on embryonic development, survival and growth of threatened catfish, *Ompok bimaculatus* early larvae. *Journal of Fish Biology*, *97*, 740–752.
- Arechavala-Lopez, P., Caballero-Froilán, J. C., Jiménez-García, M., Capó, X., Tejada, S., Saraiva, J. L., ... Moranta, D. (2020). Enriched environments enhance cognition, exploratory behaviour and brain physiological functions of *Sparus aurata*. *Scientific Reports*, *10*, 11252.
- Arechavala-Lopez, P., Diaz-Gil, C., Saraiva, J. L., Moranta, D., Castanheira, M. F., Nuñez-Velázquez, S., ... Grau, A. (2019). Effects of structural environmental enrichment on welfare of juvenile seabream (*Sparus aurata*). *Aquaculture Reports*, *15*, 100224.
- Barber, I. (2007). Parasites, behaviour and welfare in fish. *Applied Animal Behaviour Science*, *104*, 251–264.
- Barber, I., Mora, A. B., Payne, E. M., Weinersmith, K. L., & Sih, A. (2017). Parasitism, personality and cognition in fish. *Behavioural Processes*, *141*, 205–219.
- Barcellos, H. H. A., Koakoski, G., Chaulat, F., Kirsten, K. S., Kreutz, L. C., Kaluff, A. V., & Barcellos, L. J. G. (2018). The effects of auditory enrichment on zebrafish behavior and physiology. *PeerJ*, *6*, e5162.
- Barley, A. J., & Coleman, R. M. (2010). Habitat structure directly affects aggression in convict cichlids *Archocentrus nigrofasciatus*. *Current Zoology*, *56*, 52–56.
- Batzina, A., & Karakatsouli, N. (2012). The presence of substrate as a means of environmental enrichment in intensively reared gilthead seabream *Sparus aurata*: Growth and behavioral effects. *Aquaculture*, *370–371*, 54–60.
- Bayani, D.-M., Taborsky, M., & Frommen, J. G. (2017). To pee or not to pee: Urine signals mediate aggressive interactions in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behavioral Ecology and Sociobiology*, *71*, 37.
- Berbel-Filho, W. M., Rodríguez-Barreto, D., Berry, N., Leaniz, C. G. D., & Consuegra, S. (2019). Contrasting DNA methylation responses of inbred fish lines to different rearing environments. *Epigenetics*, *14*, 939–948.
- Berejikian, B. A. (2011). Rearing in enriched hatchery tanks improves dorsal fin quality of juvenile steelhead. *North American Journal of Aquaculture*, *67*, 289–293.
- Bergendahl, I. A., Miller, S., DePasquale, C., Giralico, L., & Braithwaite, V. A. (2017). Becoming a better swimmer: Structural complexity enhances agility in a captive-reared fish. *Journal of Fish Biology*, *90*, 1112–1117.
- Bergendahl, I. A., Salvanes, A. G. V., & Braithwaite, V. A. (2016). Determining the effects of duration and recency of exposure to environmental enrichment. *Applied Animal Behaviour Science*, *176*, 163–169.
- Boerrigter, J. G. J., van den Bos, R., van de Vis, H., Spanings, T., & Flik, G. (2016). Effects of density, PVC-tubes and feeding time on growth, stress and aggression in African catfish (*Clarias gariepinus*). *Aquaculture Research*, *47*, 2553–2568.
- Boeuf, G., & Le Bail, P.-Y. (1999). Does light have an influence on fish growth? *Aquaculture*, *177*, 129–152.
- Boltaña, S., Rey, S., Roher, N., Vargas, R., Huerta, M., Huntingford, F. A., ... MacKenzie, S. (2013). Behavioural fever is a synergic signal amplifying the innate immune response. *Proceedings of the Royal Society B*, *280*, 20131381.
- Bonaldo, A., Marco, P. D., Petochi, T., Marino, G., Parma, L., Fontanillas, R., ... Gatta, P. P. (2015). Feeding turbot juveniles *Psetta maxima* L. with increasing dietary plant protein levels affects growth performance and fish welfare. *Aquaculture Nutrition*, *21*, 401–413.
- Bose, A. P. H., Windorfer, J., Böhm, A., Ronco, F., Indermaur, A., Salzburger, W., & Jordan, A. (2020). Structural manipulations of a shelter resource reveal underlying preference functions in a shell-dwelling cichlid fish. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20200127.

- Braasch, I., Peterson, S. M., Desvignes, T., McCluskey, B. M., Batzel, P., & Postlethwait, J. H. (2015). A new model army: Emerging fish models to study the genomics of vertebrate Evo-Devo. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324, 316–341.
- Braithwaite, V. A., & Bergendahl, I. A. (2020). The effects of early life experience on behavioural development in captive fish species. In T. S. Kristiansen, A. Fernö, M. A. Pavlidis, & H. van de Vis (Eds.), *The welfare of fish* (Animal welfare) (pp. 111–127). Cham: Springer International Publishing.
- Brockmark, S., Neregård, L., Bohlin, T., Björnsson, B. T., & Johnsson, J. I. (2007). Effects of rearing density and structural complexity on the pre- and postrelease performance of Atlantic salmon. *Transactions of the American Fisheries Society*, 136, 1453–1462.
- Browman, H. I., Cooke, S. J., Cowx, I. G., Derbyshire, S. W. G., Kasumyan, A., Key, B., ... Arlinghaus, R. (2018). Welfare of aquatic animals: Where things are, where they are going, and what it means for research, aquaculture, recreational angling, and commercial fishing. *ICES Journal of Marine Science*, 76, 82–92.
- Browman, H. I., & Marcotte, B. M. (1987). Effects of prey color and background color on feeding by Atlantic salmon alevins. *The Progressive Fish-Culturist*, 49, 140–143.
- Brown, C., Davidson, T., & Laland, K. N. (2003). Environmental enrichment and prior experience of live prey improve foraging behaviour in hatchery-reared Atlantic salmon. *Journal of Fish Biology*, 63, 187–196.
- Brydges, N. M., & Braithwaite, V. A. (2009). Does environmental enrichment affect the behaviour of fish commonly used in laboratory work? *Applied Animal Behaviour Science*, 118, 137–143.
- Bui, S., Oppedal, F., Sievers, M., & Dempster, T. (2019). Behaviour in the toolbox to outsmart parasites and improve fish welfare in aquaculture. *Reviews in Aquaculture*, 11, 168–186.
- Burns, J. G., Saravanan, A., & Rodd, F. H. (2009). Rearing environment affects the brain size of guppies: Lab-reared guppies have smaller brains than wild-caught guppies. *Ethology*, 115, 122–133.
- Camacho, C., & Hendry, A. P. (2020). Matching habitat choice: It's not for everyone. *Oikos*, 129, 689–699.
- Carbia, P. S., & Brown, C. (2019). Environmental enrichment influences spatial learning ability in captive-reared intertidal gobies (*Bathygobius cocosensis*). *Animal Cognition*, 22, 89–98.
- Cerri, R. D. (1983). The effect of light intensity on predator and prey behaviour in cyprinid fish: Factors that influence prey risk. *Animal Behaviour*, 31, 736–742.
- Chamberlain, A. C., & Ioannou, C. C. (2019). Turbidity increases risk perception but constrains collective behaviour during foraging by fish shoals. *Animal Behaviour*, 156, 129–138.
- Champneys, T., Genner, M. J., & Ioannou, C. C. (2020). Invasive Nile tilapia dominates a threatened indigenous tilapia in competition over shelter. *Hydrobiologia*. <https://doi.org/10.1007/s10750-020-04341-8>.
- Chrétien, E., Cooke, S. J., & Boisclair, D. (2021). Does shelter influence the metabolic traits of a teleost fish? *Journal of Fish Biology*. <https://doi.org/10.1111/jfb.14653>.
- Cogliati, K. M., Herron, C. L., Noakes, D. L. G., & Schreck, C. B. (2019). Reduced stress response in juvenile Chinook salmon reared with structure. *Aquaculture*, 504, 96–101.
- Cogliati, K. M., Unrein, J. R., Schreck, C. B., & Noakes, D. L. G. (2019). Rearing environment affects spatial learning in juvenile Chinook salmon *Oncorhynchus tshawytscha*. *Journal of Fish Biology*, 95, 870–880.
- Collimore, C., Tolwani, R. J., & Rasmussen, S. (2015). The behavioral effects of single housing and environmental enrichment on adult zebrafish (*Danio rerio*). *Journal of the American Association for Laboratory Animal Science*, 54, 280–285.
- Conceição, L. E. C., Aragão, C., Dias, J., Costas, B., Terova, G., Martins, C., & Tort, L. (2012). Dietary nitrogen and fish welfare. *Fish Physiology and Biochemistry*, 38, 119–141.
- Crank, K. M., Kientz, J. L., & Barnes, M. E. (2019). An evaluation of vertically suspended environmental enrichment structures during rainbow trout rearing. *North American Journal of Aquaculture*, 81, 94–100.
- da Silva, A., Lima, M. R., Meletti, P. C., & Jerep, F. C. (2020). Impact of environmental enrichment and social group size in the aggressiveness and foraging activity of *Serrapinnus notomelas*. *Applied Animal Behaviour Science*, 224, 104943.
- de Azevedo, C. S., Cipreste, C. F., & Young, R. J. (2007). Environmental enrichment: A GAP analysis. *Applied Animal Behaviour Science*, 102, 329–343.
- de Oliveira, N. Y., de Sousa, O. M., Kunhen, V. V., & Sanches, E. G. (2019). Shelters influence in dusky grouper culture. *Boletim do Instituto de Pesca*, 45, e473.
- DePasquale, C., Fettle, S., Sturgill, J., & Braithwaite, V. A. (2019). The impact of flow and physical enrichment on preferences in zebrafish. *Applied Animal Behaviour Science*, 215, 77–81.
- DePasquale, C., Neuberger, T., Hirrlinger, A. M., & Braithwaite, V. A. (2016). The influence of complex and threatening environments in early life on brain size and behaviour. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152564.
- DePasquale, C., Sturgill, J., & Braithwaite, V. A. (2020). A standardized protocol for preference testing to assess fish welfare. *Journal of Visualized Experiments*, e60674. <https://doi.org/10.3791/60674>.
- Desjardins, J. K., Hofmann, H. A., & Fernald, R. D. (2012). Social context influences aggressive and courtship behavior in a cichlid fish. *PLoS One*, 7, e32781.
- Diniz, D. G., de Siqueira, L. S., Henrique, E. P., Pereira, P. D. C., Diniz, C. G., de Abreu, C. C., ... Fujimoto, R. Y. (2020). Environmental enrichment increases the number of telencephalic but not tectal cells of angelfish (*Pterophyllum scalare*): An exploratory investigation using optical fractionator. *Environmental Biology of Fishes*, 103, 847–857.
- Donnelly, W. A., & Whoriskey, F. G., Jr. (1991). Background-color acclimation of brook trout for crypsis reduces risk of predation by hooded mergansers *Lophodytes cucullatus*. *North American Journal of Fisheries Management*, 11, 206–211.
- Doran, C., Bierbach, D., & Laskowski, K. L. (2019). Familiarity increases aggressiveness among clonal fish. *Animal Behaviour*, 148, 153–159.
- dos Santos, T. G., Mussulini, B. H. M., Frangipani, L. A., & de Oliveira, D. L. (2020). Differential impact of shorter and longer periods of environmental enrichment on adult zebrafish exploratory activity (*Danio rerio*) in the novel tank paradigm. *Behavioural Processes*, 181, 104278.
- Durrer, L., Taborsky, M., & Frommen, J. G. (2020). Group-size preferences in a shoaling cichlid. *Behaviour*, 1, 1–17.
- Ellis, T., North, B., Scott, A. P., Bromage, N. R., Porter, M., & Gadd, D. (2002). The relationships between stocking density and welfare in farmed rainbow trout. *Journal of Fish Biology*, 61, 493–531.
- Evans, M. L., Hori, T. S., Rise, M. L., & Fleming, I. A. (2015). Transcriptomic responses of Atlantic salmon (*Salmo salar*) to environmental enrichment during juvenile rearing. *PLoS One*, 10, e0118378.
- Favero Neto, J., & Giaquinto, P. C. (2020). Environmental enrichment techniques and tryptophan supplementation used to improve the quality of life and animal welfare of Nile tilapia. *Aquaculture Reports*, 17, 100354.
- Fernö, A., Bjelland, O., & Kristiansen, T. S. (2020). The diverse world of fishes. In T. S. Kristiansen, A. Fernö, M. A. Pavlidis, & H. van de Vis (Eds.), *The welfare of fish* (Animal welfare) (pp. 43–72). Cham: Springer International Publishing.
- Finstad, A. G., Einum, S., Forseth, T., & Ugedal, O. (2007). Shelter availability affects behaviour, size-dependent and mean growth of juvenile Atlantic salmon. *Freshwater Biology*, 52, 1710–1718.
- Fischer, S., & Frommen, J. G. (2013). Eutrophication alters social preferences in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, 67, 293–299.

- Fong, S., Buechel, S. D., Boussard, A., Kotschal, A., & Kolm, N. (2019). Plastic changes in brain morphology in relation to learning and environmental enrichment in the guppy (*Poecilia reticulata*). *Journal of Experimental Biology*, 222(10).
- Gabagambi, N. P., Salvanes, A. G. V., Midtøy, F., & Skorping, A. (2019). The tapeworm ligula intestinalis alters the behavior of the fish intermediate host *Engraulicypris sardella*, but only after it has become infective to the final host. *Behavioural Processes*, 158, 47–52.
- Giacomini, A. C. V. V., Abreu, M. S., Zanandrea, R., Saibt, N., Friedrich, M. T., Koakoski, G., ... Barcellos, L. J. G. (2016). Environmental and pharmacological manipulations blunt the stress response of zebrafish in a similar manner. *Scientific Reports*, 6, 1–6.
- Greenway, E., Jones, K. S., & Cooke, G. M. (2016). Environmental enrichment in captive juvenile thornback rays, *Raja clavata* (Linnaeus 1758). *Applied Animal Behaviour Science*, 182, 86–93.
- Greenwood, M. F. D., & Metcalfe, N. B. (1998). Minnows become nocturnal at low temperatures. *Journal of Fish Biology*, 53, 25–32.
- Helfman, G. S., Collette, B. B., Facey, D. E., & Bowen, B. W. (2009). *The diversity of fishes: Biology, evolution, and ecology* (2nd ed.). New Jersey, NJ: Wiley-Blackwell.
- Huntingford, F., & Kadri, S. (2013). Exercise, stress and welfare. In A. P. Palstra & J. V. Planas (Eds.), *Swimming physiology of fish: Towards using exercise to farm a fit fish in sustainable aquaculture* (pp. 161–174). Berlin, Heidelberg: Springer.
- Huntingford, F. A. (2004). Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *Journal of Fish Biology*, 65, 122–142.
- Huntingford, F. A., Adams, C., Braithwaite, V. A., Kadri, S., Pottinger, T. G., Sandøe, P., & Turnbull, J. F. (2006). Current issues in fish welfare. *Journal of Fish Biology*, 68, 332–372.
- Huntingford, F. A., Rey, S., & Quaggiotto, M.-M. (2020). Behavioural fever, fish welfare and what farmers and fishers know. *Applied Animal Behaviour Science*, 231, 105090.
- Huse, I., Bjordal, Å., Fernö, A., & Furevik, D. (1990). The effect of shading in pen rearing of Atlantic salmon (*Salmo salar*). *Aquacultural Engineering*, 9, 235–244.
- Hyvärinen, P., & Rodewald, P. (2013). Enriched rearing improves survival of hatchery-reared Atlantic salmon smolts during migration in the River Tornionjoki. *Canadian Journal of Fisheries and Aquatic Sciences*, 70, 1386–1395.
- Isaza, D. F. G., Cramp, R. L., & Franklin, C. E. (2020). Thermal acclimation offsets the negative effects of nitrate on aerobic scope and performance. *Journal of Experimental Biology*, 223(16), jeb224444.
- Jacobs, A., Doran, C., Murray, D. S., Telsnig, J. D., Laskowski, K. L., Jones, N. A. R., ... Præbel, K. (2018). On the challenges and opportunities facing fish biology: A discussion of five key knowledge gaps. *Journal of Fish Biology*, 92, 690–698.
- Johnson, Z. V., Moore, E. C., Wong, R. Y., Godwin, J. R., Strelman, J. T., & Roberts, R. B. (2020). Exploratory behaviour is associated with microhabitat and evolutionary radiation in Lake Malawi cichlids. *Animal Behaviour*, 160, 121–134.
- Johnsson, J. I., Brockmark, S., & Näslund, J. (2014). Environmental effects on behavioural development consequences for fitness of captive-reared fishes in the wild. *Journal of Fish Biology*, 85, 1946–1971.
- Jones, N. A. R., & Magurran, A. E. (2014). Aggression in captivity and the implication for interspecific aggression between once sympatric species of Mexican goodeid. *Pan-American Journal of Aquatic Sciences*, 9, 179–187.
- Jones, N. A. R., Spence, R., Jones, F. A. M., & Spence-Jones, H. C. (2019). Shade as enrichment: Testing preferences for shelter in two model fish species. *Journal of Fish Biology*, 95, 1161–1165.
- Josi, D., Taborsky, M., & Frommen, J. G. (2018). Habitat preferences depend on substrate quality in a cooperative breeder. *Evolutionary Ecology Research*, 19, 503–516.
- Kalleberg, H. (1958). Observations in a stream tank of territoriality and competition in juvenile salmon and trout. *Report of Institute of Freshwater Research, Drottningholm*, 39, 55–98.
- Keep, J. K., Watson, J. R., Cramp, R. L., Jones, M. J., Gordos, M. A., Ward, P. J., & Franklin, C. E. (2020). Low light intensities increase avoidance behaviour of diurnal fish species: Implications for use of road culverts by fish. *Journal of Fish Biology*, 98(3), 634–642.
- Kelley, J. L., Magurran, A. E., & Macías García, C. (2006). Captive breeding promotes aggression in an endangered Mexican fish. *Biological Conservation*, 133, 169–177.
- Kientz, J. L., & Barnes, M. E. (2016). Structural complexity improves the rearing performance of rainbow trout in circular tanks. *North American Journal of Aquaculture*, 78, 203–207.
- King, T. A. (2019). Wild caught ornamental fish: A perspective from the UK ornamental aquatic industry on the sustainability of aquatic organisms and livelihoods. *Journal of Fish Biology*, 94, 925–936.
- Kistler, C., Heggin, D., Würbel, H., & König, B. (2011). Preference for structured environment in zebrafish (*Danio rerio*) and checker barbs (*Puntius oligolepis*). *Applied Animal Behaviour Science*, 135, 318–327.
- Knopf, K., Buschmann, K., Hansel, M., Radinger, J., & Kloas, W. (2018). Flash photography does not induce stress in the Ram cichlid *Mikrogeophagus ramirezi* (Myers & Harry, 1948) in aquaria. *Journal of Applied Ichthyology*, 34, 922–928.
- Kochhann, D., & Val, A. L. (2017). Social hierarchy and resting metabolic rate in the dwarf cichlid *Apistogramma agassizii*: The role of habitat enrichment. *Hydrobiologia*, 789, 123–131.
- Krueger, L. D., Thurston, S. E., Kirk, J., Elsaiedi, F., Freeman, Z. T., Goldman, D., ... Keller, J. M. (2020). Enrichment Preferences of Singly Housed Zebrafish (*Danio rerio*). Retrieved from <https://www.ingentaconnect.com/content/aalas/jaalas/2020/00000059/00000002/art00006>
- Laland, K. N., Atton, N., & Webster, M. M. (2011). From fish to fashion: Experimental and theoretical insights into the evolution of culture. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 366, 958–968.
- Lee, C. J., Paull, G. C., & Tyler, C. R. (2019). Effects of environmental enrichment on survivorship, growth, sex ratio and behaviour in laboratory maintained zebrafish *Danio rerio*. *Journal of Fish Biology*, 94, 86–95.
- Lee, C. J., Tyler, C. R., & Paull, G. C. (2018). Can simple tank changes benefit the welfare of laboratory zebrafish *Danio rerio*? *Journal of Fish Biology*, 92, 653–659.
- Lehtonen, T. K., & Wong, B. B. M. (2020). Context-dependent resource choice in a nest-building fish. *Animal Behaviour*, 166, 297–303.
- Lidster, K., Readman, G. D., Prescott, M. J., & Owen, S. F. (2017). International survey on the use and welfare of zebrafish *Danio rerio* in research. *Journal of Fish Biology*, 90, 1891–1905.
- Lorenzen, K., Leber, K. M., & Blankenship, H. L. (2010). Responsible approach to marine stock enhancement: An update. *Reviews in Fisheries Science*, 18, 189–210.
- MacIntyre, C. M., Ellis, T., North, B. P., & Turnbull, J. F. (2008). The influences of water quality on the welfare of farmed rainbow trout: A review. In E. J. Branson (Ed.), *Fish welfare* (pp. 150–184). New Jersey, NJ: Wiley-Blackwell.
- Maia, C. M., & Volpato, G. L. (2018). Individuality matters for substrate-size preference in the Nile tilapia juveniles. *Journal of Applied Animal Welfare Science*, 21, 316–324.
- Makino, H., Masuda, R., & Tanaka, M. (2015). Environmental stimuli improve learning capability in striped knifejaw juveniles: The stage-specific effect of environmental enrichment and the comparison between wild and hatchery-reared fish. *Fisheries Science*, 81, 1035–1042.
- Manuel, R., Gorissen, M., Stokkermans, M., Zethof, J., Ebbesson, L. O. E., van de Vis, H., ... van den Bos, R. (2015). The effects of environmental

- enrichment and age-related differences on inhibitory avoidance in zebrafish (*Danio rerio* Hamilton). *Zebrafish*, 12, 152–165.
- Marcon, M., Mocelin, R., Benvenuti, R., Costa, T., Herrmann, A. P., de Oliveira, D. L., ... Piato, A. (2018). Environmental enrichment modulates the response to chronic stress in zebrafish. *Journal of Experimental Biology*, 221, jeb176735.
- Marcon, M., Mocelin, R., Sachett, A., Siebel, A. M., Herrmann, A. P., & Piato, A. (2018). Enriched environment prevents oxidative stress in zebrafish submitted to unpredictable chronic stress. *PeerJ*, 6, e5136.
- Martins, C. I. M., Galhardo, L., Noble, C., Damsgård, B., Spedicato, M. T., Zupa, W., ... Kristiansen, T. (2012). Behavioural indicators of welfare in farmed fish. *Fish Physiology and Biochemistry*, 38, 17–41.
- Mason, G. J. (2010). Species differences in responses to captivity: Stress, welfare and the comparative method. *Trends in Ecology & Evolution*, 25, 713–721.
- Masud, N., Ellison, A., Pope, E. C., & Cable, J. (2020). Cost of a deprived environment – increased intraspecific aggression and susceptibility to pathogen infections. *Journal of Experimental Biology*, 20.
- McCartt, A. L., Lynch, W. E., & Johnson, D. L. (1997). How light, a predator, and experience influence bluegill use of shade and schooling. *Environmental Biology of Fishes*, 49, 79–87.
- McRobert, S. P., Kiesel, A. L., Sneker, J. L., & Ruhl, N. (2012). Behavioural syndromes and shoaling: Connections between aggression, boldness and social behaviour in three different Danios. *Behaviour*, 149, 1155–1175.
- Mes, D., van Os, R., Gorissen, M., Ebbesson, L. O. E., Finstad, B., Mayer, I., & Vindas, M. A. (2019). Effects of environmental enrichment on forebrain neural plasticity and survival success of stocked Atlantic salmon. *Journal of Experimental Biology*, 222, jeb212258.
- Millidine, K. J., Armstrong, J. D., & Metcalfe, N. B. (2006). Presence of shelter reduces maintenance metabolism of juvenile salmon. *Functional Ecology*, 20, 839–845.
- Murtaza, M., Ul, H., Zuberi, A., Ahmad, M., Amir, I., Kamran, M., & Ahmad, M. (2020). Influence of early rearing environment on waterborne cortisol and expression of stress-related genes in grass carp (*Ctenopharyngodon idella*). *Molecular Biology Reports*, 47, 5051–5060.
- Muschick, M., Indermaur, A., & Salzburger, W. (2012). Convergent evolution within an adaptive radiation of cichlid fishes. *Current Biology*, 22, 2362–2368.
- Näslund, J., & Johnsson, J. I. (2014). Environmental enrichment for fish in captive environments: Effects of physical structures and substrates. *Fish and Fisheries*, 17, 1–30.
- Näslund, J., Rosengren, M., Del Villar, D., Gansel, L., Norrgård, J. R., Persson, L., ... Kvingedal, E. (2013). Hatchery tank enrichment affects cortisol levels and shelter-seeking in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 70, 585–590.
- Näslund, J., Rosengren, M., & Johnsson, J. I. (2019). Fish density, but not environmental enrichment, affects the size of cerebellum in the brain of juvenile hatchery-reared Atlantic salmon. *Environmental Biology of Fishes*, 102, 705–712.
- Nay, T. J., Johansen, J. L., Rummer, J. L., Steffensen, J. F., Pratchett, M. S., & Hoey, A. S. (2020). Habitat complexity influences selection of thermal environment in a common coral reef fish. *Conservation Physiology*, 8, coaa070.
- Newberry, R. C. (1995). Environmental enrichment: Increasing the biological relevance of captive environments. *Applied Animal Behaviour Science*, 44, 229–243.
- Olivotto, I., Rollo, A., Sulpizio, R., Avella, M., Tosti, L., & Carnevali, O. (2006). Breeding and rearing the Sunrise Dottyback *Pseudochromis flavivertex*: The importance of live prey enrichment during larval development. *Aquaculture*, 255, 480–487.
- Ostrowski, A. C. (1989). Effect of rearing tank background color on early survival of dolphin larvae. *The Progressive Fish-Culturist*, 51, 161–163.
- Pereira, P. D. C., Henrique, E. P., Porfírio, D. M., Crispim, C. C. D. S., Campos, M. T. B., de Oliveira, R. M., ... Diniz, D. G. (2020). Environmental enrichment improved learning and memory, increased telencephalic cell proliferation, and induced differential gene expression in *Collossoma macropomum*. *Frontiers in Pharmacology*, 11.
- Perrone, R., Pedraja, F., Valiño, G., Tassino, B., & Silva, A. (2019). Non-breeding territoriality and the effect of territory size on aggression in the weakly electric fish, *Gymnotus omarorum*. *Acta Ethologica*, 22, 79–89.
- Petersen, M. F., & Steffensen, J. F. (2003). Preferred temperature of juvenile Atlantic cod *Gadus morhua* with different haemoglobin genotypes at normoxia and moderate hypoxia. *Journal of Experimental Biology*, 206, 359–364.
- Pounder, K. C., Mitchell, J. L., Thomson, J. S., Pottinger, T. G., Buckley, J., & Sneddon, L. U. (2016). Does environmental enrichment promote recovery from stress in rainbow trout? *Applied Animal Behaviour Science*, 176, 136–142.
- Powers, D. A. (1989). Fish as model systems. *Science*, 246, 352–358.
- Pritchard, V. L., Lawrence, J., Butlin, R. K., & Krause, J. (2001). Shoal choice in zebrafish, *Danio rerio*: The influence of shoal size and activity. *Animal Behaviour*, 62, 1085–1088.
- Rae, D. L., Mos, B., Scott, A., & Dworjanyn, S. A. (2020). Training fish for restocking: Refuge and predator training in the hatchery has limited benefits for a marine fish. *Journal of Fish Biology*, 97, 172–182.
- Rahman, M. M., Nur, N., Mahmud-Al-Hasan, M., Asaduzzaman, S., Rouf, M. A., & Rahman, S. M. (2020). Effects of light and artificial fish shelter (PVC pipe) on some phenotypic traits of stinging catfish (*Heteropneustes fossilis* Bloch, 1794). *Aquaculture Research*, 51, 124–134.
- Räihä, V., Sundberg, L.-R., Ashrafi, R., Hyvärinen, P., & Karvonen, A. (2019). Rearing background and exposure environment together explain higher survival of aquaculture fish during a bacterial outbreak. *Journal of Applied Ecology*, 56, 1741–1750.
- Reiser, S., Pohlmann, D. M., Koops, U., Gröger, J. P., & Focken, U. (2019). Using gravel for environmental enrichment in salmonid hatcheries: The effect of gravel size during egg incubation, endogenous and first feeding in rainbow trout. *Journal of Applied Ichthyology*, 35, 465–472.
- Rodriguez-Pinto, I. I., Rieucou, G., Handegard, N. O., & Boswell, K. M. (2020). Environmental context elicits behavioural modification of collective state in schooling fish. *Animal Behaviour*, 165, 107–116.
- Rosengren, M., Kvingedal, E., Näslund, J., Johnsson, J. I., & Sundell, K. (2016). Born to be wild: Effects of rearing density and environmental enrichment on stress, welfare, and smolt migration in hatchery-reared Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 74, 396–405.
- Roy, T., & Bhat, A. (2016). Learning and memory in juvenile zebrafish: What makes the difference – population or rearing environment? *Ethology*, 122, 308–318.
- Ruyet, J. P. L., Alexandre, J. C., Thébaud, L., & Mugnier, C. (1993). Marine fish larvae feeding: Formulated diets or live prey? *Journal of the World Aquaculture Society*, 24, 211–224.
- Salvanes, A. G. V., & Braithwaite, V. (2006). The need to understand the behaviour of fish reared for mariculture or restocking. *ICES Journal of Marine Science*, 63, 345–354.
- Salvanes, A. G. V., Moberg, O., Ebbesson, L. O. E., Nilsen, T. O., Jensen, K. H., & Braithwaite, V. A. (2013). Environmental enrichment promotes neural plasticity and cognitive ability in fish. *Proceedings of the Royal Society B*, 280, 20131331.
- Sanhueza, N., Donoso, A., Aguilar, A., Farlora, R., Carnicero, B., Míguez, J. M., ... Boltana, S. (2018). Thermal modulation of monoamine levels influence fish stress and welfare. *Frontiers in Endocrinology*, 9. <https://doi.org/10.3389/fendo.2018.00717>.
- Santon, M., Bitton, P.-P., Dehm, J., Fritsch, R., Harant, U. K., Anthes, N., & Michiels, N. K. (2020). Redirection of ambient light improves predator

- detection in a diurnal fish. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20192292.
- Saraiva, J. L., Arechavala-Lopez, P., Castanheira, M. F., Volstorf, J., & Heinzpeter Studer, B. (2019). A global assessment of welfare in farmed fishes: The FishEthoBase. *Fishes*, 4, 30.
- Saraiva, S. D. O., & Pompeu, P. S. (2016). The effect of structural enrichment in hatchery tanks on the morphology of two neotropical fish species. *Neotropical Ichthyology*, 12, 891–901.
- Saxby, A., Adams, L., Snellgrove, D., Wilson, R. W., & Sloman, K. A. (2010). The effect of group size on the behaviour and welfare of four fish species commonly kept in home aquaria. *Applied Animal Behaviour Science*, 125, 195–205.
- Schartl, M. (2014). Beyond the zebrafish: Diverse fish species for modeling human disease. *Disease Models & Mechanisms*, 7, 181–192.
- Schroeder, P., Jones, S., Young, I. S., & Sneddon, L. U. (2014). What do zebrafish want? Impact of social grouping, dominance and gender on preference for enrichment. *Laboratory Animals*, 48, 328–337.
- Shepherdson, D. J., Mellen, J. D., & Hutchins, M. (1999). *Second nature: Environmental enrichment for captive animals*. London: Smithsonian Institution.
- Skandalis, D. A., Dobell, C. D., Shaw, J. C., & Tattersall, G. J. (2020). Hydrogen sulfide exposure reduces thermal set point in zebrafish. *Royal Society Open Science*, 7, 200416.
- Sloman, K. A., Baldwin, L., McMahon, S., & Snellgrove, D. (2011). The effects of mixed-species assemblage on the behaviour and welfare of fish held in home aquaria. *Applied Animal Behaviour Science*, 135, 160–168.
- Sloman, K. A., Bouyoucos, I. A., Brooks, E. J., & Sneddon, L. U. (2019). Ethical considerations in fish research. *Journal of Fish Biology*, 94, 556–577.
- Smith, A. J., Clutton, R. E., Lilley, E., Hansen, K. E. A., & Brattelid, T. (2018). PREPARE: Guidelines for planning animal research and testing. *Laboratory Animals*, 52, 135–141.
- Smith, C. (2011). Good fences make good neighbours: The role of landmarks in territory partitioning in the rose bitterling (*Rhodeus ocellatus*). *Behaviour*, 148, 233–246.
- Sneddon, L. U., Halsey, L. G., & Bury, N. R. (2017). Considering aspects of the 3Rs principles within experimental animal biology. *Journal of Experimental Biology*, 220, 3007–3016.
- Sneddon, L. U., Wolfenden, D. C. C., & Thomson, J. S. (2016). 12 - stress management and welfare. In C. B. Schreck, L. Tort, A. P. Farrell, & C. J. Brauner (Eds.), *Fish Physiology: Biology of Stress in Fish* (pp. 463–539). Academic Press.
- Soares, S. M., Kirsten, K., Pompermaier, A., Maffi, V. C., Koakoski, G., Woloszyn, M., ... Barcellos, L. J. G. (2020). Sex segregation affects exploratory and social behaviors of zebrafish according to controlled housing conditions. *Physiology & Behavior*, 222, 112944.
- Solas, M. R., Skoglund, H., & Salvanes, A. G. V. (2019). Can structural enrichment reduce predation mortality and increase recaptures of hatchery-reared Atlantic salmon *Salmo salar* L. fry released into the wild? *Journal of Fish Biology*, 95, 575–588.
- Spence, R., Fatema, M. K., Reichard, M., Huq, K. A., Wahab, M. A., Ahmed, Z. F., & Smith, C. (2006). The distribution and habitat preferences of the zebrafish in Bangladesh. *Journal of Fish Biology*, 69, 1435–1448.
- Spence, R., Gerlach, G., Lawrence, C., & Smith, C. (2008). The behaviour and ecology of the zebrafish, *Danio rerio*. *Biological Reviews*, 83, 13–34.
- Steendam, C., Verhelst, P., Wassenbergh, S. V., & Meyer, J. D. (2020). Burrowing behaviour of the European eel (*Anguilla Anguilla*): Effects of life stage. *Journal of Fish Biology*, 97, 1332–1342.
- Stevens, C. H., Croft, D. P., Paull, G. C., & Tyler, C. R. (2017). Stress and welfare in ornamental fishes: What can be learned from aquaculture? *Journal of Fish Biology*, 91, 409–428.
- Stevens, C. H., Reed, B. T., & Hawkins, P. (2021). Enrichment for laboratory zebrafish—A review of the evidence and the challenges. *Animals*, 11, 698.
- Strand, D. A., UtnePalm, A. C., Jakobsen, P. J., Braithwaite, V. A., Jensen, K. H., & Salvanes, A. G. V. (2010). Enrichment promotes learning in fish. *Marine Ecology Progress Series*, 412, 273–282.
- Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., ... Edgar, G. J. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, 501, 539–542.
- Sullivan, M., Lawrence, C., & Blache, D. (2016). Why did the fish cross the tank? Objectively measuring the value of enrichment for captive fish. *Applied Animal Behaviour Science*, 174, 181–188.
- Sumner, F. B. (1934). Does “protective coloration” protect?—Results of some experiments with fishes and birds. *Proceedings of the National Academy of Sciences of the United States of America*, 20, 559–564.
- Sundström, L. F., & Johnsson, J. I. (2001). Experience and social environment influence the ability of young brown trout to forage on live novel prey. *Animal Behaviour*, 61, 249–255.
- Swaigood, R. R. (2007). Current status and future directions of applied behavioral research for animal welfare and conservation. *Applied Animal Behaviour Science*, 102, 139–162.
- Sykes, D. J., Suriyampola, P. S., & Martins, E. P. (2018). Recent experience impacts social behavior in a novel context by adult zebrafish (*Danio rerio*). *PLoS One*, 13, e0204994.
- Tatara, C. P., Riley, S. C., & Scheurer, J. A. (2009). Growth, survival, and habitat use of naturally reared and hatchery steelhead fry in streams: Effects of an enriched hatchery rearing environment. *Transactions of the American Fisheries Society*, 138, 441–457.
- Thoré, E. S. J., Brendonck, L., & Pinceel, T. (2020). Conspecific density and environmental complexity impact behaviour of Turquoise killifish (*Nothobranchius furzeri*). *Journal of Fish Biology*, 97, 1448–1461.
- Tian, H.-Y., Zhang, D.-D., Xu, C., Wang, F., & Liu, W.-B. (2015). Effects of light intensity on growth, immune responses, antioxidant capability and disease resistance of juvenile blunt snout bream *Megalobrama amblycephala*. *Fish & Shellfish Immunology*, 47, 674–680.
- Toli, E. A., Noreikiene, K., DeFaveri, J., & Merilä, J. (2017). Environmental enrichment, sexual dimorphism, and brain size in sticklebacks. *Ecology and Evolution*, 7, 1691–1698.
- Toni, M., Manciocco, A., Angiulli, E., Alleva, E., Cioni, C., & Malavasi, S. (2019). Review: Assessing fish welfare in research and aquaculture, with a focus on European directives. *Animal*, 13, 161–170.
- Torrezani, C. S., Pinho-Neto, C. F., Miyai, C. A., Sanches, F. H. C., & Barreto, R. E. (2013). Structural enrichment reduces aggression in *Tilapia rendalli*. *Marine and Freshwater Behaviour and Physiology*, 46, 183–190.
- Turnbull, J. F., & Huntingford, F. A. (2012). Welfare and aquaculture: Where benefish fits in. *Aquaculture Economics & Management*, 16, 433–440.
- Ullah, I., Zuberi, A., Khan, K. U., Ahmad, S., Thörnqvist, P.-O., & Winberg, S. (2017). Effects of enrichment on the development of behaviour in an endangered fish mahseer (*Tor putitora*). *Applied Animal Behaviour Science*, 186, 93–100.
- Ullah, I., Zuberi, A., Rehman, H., Ali, Z., Thörnqvist, P.-O., & Winberg, S. (2020). Effects of early rearing enrichments on modulation of brain monoamines and hypothalamic–pituitary–interrenal axis (HPI axis) of fish mahseer (*Tor putitora*). *Fish Physiology and Biochemistry*, 46, 75–88.
- Utne-Palm, A. C., & Hart, P. J. B. (2000). The effects of familiarity on competitive interactions between threespined sticklebacks. *Oikos*, 91, 225–232.
- Utne-Palm, A. C., & Smith, A. (2020). Fish as laboratory animals. In T. S. Kristiansen, A. Fernö, M. A. Pavlidis, & H. van de Vis (Eds.), *The welfare of fish (Animal Welfare)* (pp. 375–400). Switzerland: Springer International Publishing.
- Valdimarsson, S. K., & Metcalfe, N. B. (1998). Shelter selection in juvenile Atlantic salmon, or why do salmon seek shelter in winter? *Journal of Fish Biology*, 52, 42–49.

- Valdimarsson, S. K., & Metcalfe, N. B. (2001). Is the level of aggression and dispersion in territorial fish dependent on light intensity? *Animal Behaviour*, *61*, 1143–1149.
- Vanderzwalmen, M., Carey, P., Snellgrove, D., & Sloman, K. A. (2020). Benefits of enrichment on the behaviour of ornamental fishes during commercial transport. *Aquaculture*, *526*, 735360.
- Vanderzwalmen, M., McNeill, J., Delieuvin, D., Senes, S., Sanchez-Lacalle, D., Mullen, C., ... Sloman, K. A. (2021). Monitoring water quality changes and ornamental fish behaviour during commercial transport. *Aquaculture*, *531*, 735860.
- Villamizar, N., Vera, L. M., Foulkes, N. S., & Sánchez-Vázquez, F. J. (2014). Effect of lighting conditions on zebrafish growth and development. *Zebrafish*, *11*, 173–181.
- Voorhees, J. M., Huysman, N., Krebs, E., & Barnes, M. E. (2020). Influence of water velocity and vertically-suspended structures on rainbow trout rearing performance. *Open Journal of Animal Sciences*, *10*, 152–161.
- Wafer, L. N., Jensen, V. B., Whitney, J. C., Gomez, T. H., Flores, R., & Goodwin, B. S. (2016). Effects of environmental enrichment on the fertility and fecundity of zebrafish (*Danio rerio*). *Journal of the American Association for Laboratory Animal Science*, *55*, 291–294.
- Ward, A. J. W., Duff, A. J., Krause, J., & Barber, I. (2005). Shoaling behaviour of sticklebacks infected with the microsporidian parasite, *Glugea anomala*. *Environmental Biology of Fishes*, *72*, 155–160.
- Ward, A. J. W., Kent, M. I. A., & Webster, M. M. (2020). Social recognition and social attraction in group-living fishes. *Frontiers in Ecology and Evolution*, *8*. <https://doi.org/10.3389/fevo.2020.00015>.
- Ward, A. J. W., & Webster, M. M. (2016). *Sociality: The behaviour of group living animals*. Switzerland: Springer Academic Publishing.
- Watz, J. (2019). Structural complexity in the hatchery rearing environment affects activity, resting metabolic rate and post-release behaviour in brown trout *Salmo trutta*. *Journal of Fish Biology*, *95*, 638–641.
- Webster, M. M., & Hart, P. J. B. (2004). Substrate discrimination and preference in foraging fish. *Animal Behaviour*, *68*, 1071–1077.
- Webster, M. M., & Hart, P. J. B. (2006). Kleptoparasitic prey competition in shoaling fish: Effects of familiarity and prey distribution. *Behavioral Ecology*, *17*, 959–964.
- Webster, M. M., & Hart, P. J. B. (2007). Prior association reduces kleptoparasitic prey competition in shoals of three-spined sticklebacks. *Animal Behaviour*, *74*, 253–258.
- Webster, M. M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*, *582*, 337–340.
- White, S. C., Krebs, E., Huysman, N., Voorhees, J. M., & Barnes, M. E. (2019). Use of suspended plastic conduit arrays during brown trout and rainbow trout rearing in circular tanks. *North American Journal of Aquaculture*, *81*, 101–106.
- Williams, T. D., Readman, G. D., & Owen, S. F. (2009). Key issues concerning environmental enrichment for laboratory-held fish species. *Laboratory Animals*, *43*, 107–120.
- Wong, M., & Balshine, S. (2011). Fight for your breeding right: hierarchy re-establishment predicts aggression in a social queue. *Biology Letters*, *7*, 190–193.
- Woodward, M. A., Winder, L. A., & Watt, P. J. (2019). Enrichment increases aggression in zebrafish. *Fishes*, *4*, 22.
- Wootton, R. J., & Smith, C. (2014). *Reproductive biology of teleost fishes*. Ltd: John Wiley & Sons.
- Wu, H., Li, M., Zeng, R., Liu, X., Yang, K., & Song, Z. (2020). Substrate type and brightness preference of *Schizothorax wangchiachii* and *Percocypris pingi* juveniles. *Aquaculture Research*, *51*, 2790–2798.
- Yaripour, S., Kekäläinen, J., Hyvärinen, P., Kaunisto, S., Piironen, J., Vainikka, A., ... Kortet, R. (2020). Does enriched rearing during early life affect sperm quality or skin colouration in the adult brown trout? *Aquaculture*, *529*, 735648.
- Zhang, Z., Bai, Q., Xu, X., Guo, H., & Zhang, X. (2019). Effects of environmental enrichment on the welfare of juvenile black rockfish *Sebastes schlegelii*: Growth, behavior and physiology. *Aquaculture*, *518*, 734782.
- Zhang, Z., Xu, X., Wang, Y., & Zhang, X. (2020). Effects of environmental enrichment on growth performance, aggressive behavior and stress-induced changes in cortisol release and neurogenesis of black rockfish *Sebastes schlegelii*. *Aquaculture*, *528*, 735483.
- Zimmermann, E. W., Purchase, C. F., & Fleming, I. A. (2012). Reducing the incidence of net cage biting and the expression of escape-related behaviors in Atlantic cod (*Gadus morhua*) with feeding and cage enrichment. *Applied Animal Behaviour Science*, *141*, 71–78.

How to cite this article: Jones, N. A. R., Webster, M. M., & Salvanes, A. G. V. (2021). Physical enrichment research for captive fish: Time to focus on the DETAILS. *Journal of Fish Biology*, 1–22. <https://doi.org/10.1111/jfb.14773>