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Closing the Gaps in Fish Welfare: The Case for More Fundamental Work Into Physical Enrichment

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ABSTRACT

Billions of fishes are kept in captivity for research and food production world-wide, with a strong impetus for maintaining high welfare standards. Accordingly, the importance of empirical research into the welfare and husbandry of captive fishes is increasingly acknowledged in both science and aquaculture, alongside growing public and governmental interest. Physical enrichment can have an important influence on welfare in of captive fishes, but many questions remain. Here, we summarise the current state of research and outline knowledge gaps in the area of physical enrichment, which is a fundamental aspect to improving welfare of captive fishes. To explore the level of research interest this area across time we conducted a series of surveys, using the number of papers published per year as a metric. These surveys highlight that work on fish welfare, while representing a relatively low proportion of fish research overall, is increasing rapidly. For species that are of aquaculture importance or used commonly as laboratory subjects, we show a positive relationship between general research interest and number of welfare-related papers. However, for many, particularly relatively less studied, species the proportion of papers on enrichment remains low, with a slower increase compared to welfare-related papers in general. In terms of common metrics used to quantify fish welfare, there is a reliance on growth and behaviour, with scope for inclusion and combination of a more comprehensive range of reproducible measures. We finish by highlighting recent progress, promising areas for future research and suggestions for advances in this area.

1 | Introduction

Populations of captive fishes are maintained in many contexts, from aquaculture to public and private aquariums to research. Research focusing on fish has been increasing yearly for the last 30 years (Figure 1a): alongside research into aquaculture techniques, fishes are used as model species in fields as diverse as behaviour, conservation, evolutionary biology, genetics, molecular biology, pathology, physiology, psychology and toxicology—as well as representing important species within ecological research and monitoring (Ostrander 2000; Turner 2012; Andersen 2019). With wild populations facing intensifying threats (Comte and Olden 2017; Pinsky et al. 2019), captive breeding and maintenance is also becoming increasingly important in species conservation and safeguarding. Consequently, considering and improving the welfare of captive fishes is an increasingly important objective (Williams, Readman, and Owen 2009; Saraiva and Arechavala-Lopez 2019).

Welfare, defined most generally in terms of ensuring animal health and providing what animals want, sensu (Dawkins 2017) is important for all captive animals. For research subjects specifically, it is crucial to consider for three mutually inclusive reasons. First, to ensure basic survival and health, including psychological stability (Korte, Olivier, and Koolhaas 2007). Second, to promote the biological relevance and validity of

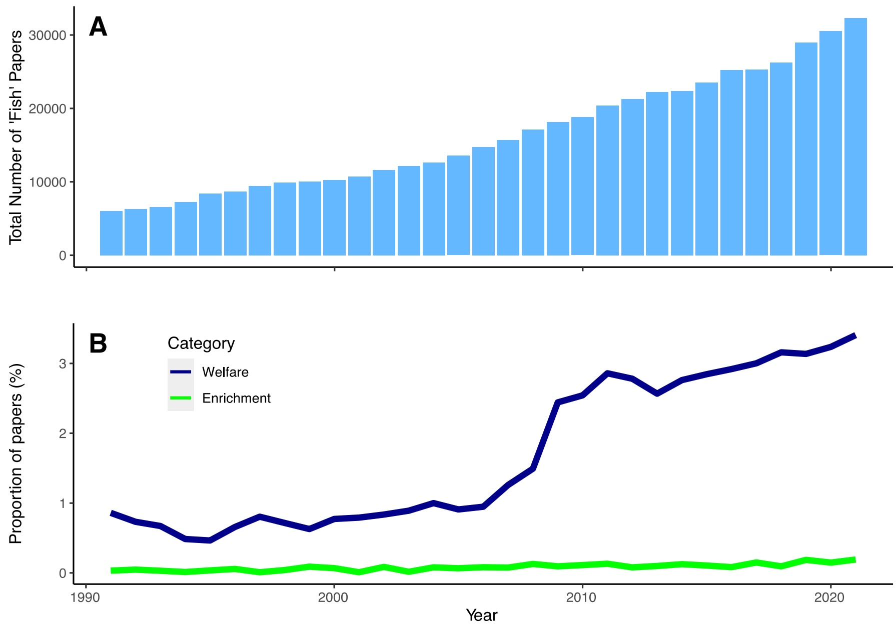

FIGURE 1 | Research interest over time for (A) fish in general (number of papers published per year) and (B) welfare- and enrichment-specific papers relative to general research levels (as a percentage of 'fish' papers published per year). See Appendix S1 for methods and full search terms used.

study results, including occurrence of 'normal' behaviour (Newberry 1995; Williams, Readman, and Owen 2009); third, to ensure that research is ethically sound and conducted as humanely as possible (Bovenkerk and Meijboom 2020). Indeed, animal welfare, including that of fishes, has been the subject of increasing interest and attention over the years (Figure 1b), and research has highlighted the need for data-driven improvements (Oldfield and Bonano 2023). The philosophical aspects of the topic—in particular the relationship between animal welfare and consciousness, sentience, emotional experiences and pain—have long debated (Chandroo, Yue, and Moccia 2004; Yue Cottee 2012; Jones 2013; Brown 2015; Sneddon et al. 2014; Lavery and Mason 2023). While academically fascinating, this debate is divisive and can be difficult to tackle empirically (Hart 2023). In light of the challenges inherent in assessing the level of sentience of any organism, we focus on welfare considerations that are not necessarily dependent on it, and on metrics that can be more practically assessed and compared: regardless of an organism's cognitive and psychological complexity, provision of optimal conditions for health and survival remains beneficial for the reasons stated above. In this article, we focus on one of the most practical and actionable aspects of fish welfare: the suitability of the physical conditions in which captive animals are housed.

There are multiple aspects of fish housing which may affect welfare and reproducibility across assays, which are often species-specific, for example, (Balzarini et al. 2014; Thomas et al. 2022; Jones et al. 2019; Zhang, Wu, et al. 2022; Jolles, Aaron Taylor, and Manica 2016): space and water quality; light and temperature; food quantity and quality; social conditions; presence of parasites or disease; and environmental enrichment (Williams, Readman, and Owen 2009). Our focus in this article is on the latter—defined as per Näslund and Johnsson (2016) as a deliberate increase in environmental complexity with the aim to reduce maladaptive traits in fishes reared in otherwise barren settings.

Environmental enrichment provision has long been known to affect fish survival (Kalleberg 1958; Robertson 1919), physiology (Millidine, Armstrong, and Metcalfe 2006; Chrétien et al. 2021) but see (Kegler et al. 2013), behaviour, brain development and cognition (Salvanes et al. 2013; Kleiber et al. 2023), and stress (Mes et al. 2019; Arambam et al. 2020). However, it has only become a topic of major focus in the last two decades, following research in other taxa highlighting the effect of barren captive environments on behaviour, welfare and validity of research data (Newberry 1995; Dawkins 1988, 1998). In practical terms, attempts to improve enrichment for all captive species, including fishes, must balance efficacy, ease of implementation and resource requirements—while taking into account the logistical challenges of standardising across laboratories. Additionally, the nature of some studies may impose limitations on the enrichment which can be implemented, such as substrates/materials which may interfere with chemistry of substances introduced as part of (long-term) toxicity studies (Williams, Readman, and Owen 2009).

2 | Aims

The aim of this article is to highlight recent progress surrounding physical enrichment for fishes and to discuss knowledge gaps and promising areas for future advances. As a basis for the article, we conducted snapshot literature surveys to provide a high-level comparison of research effort and focus across time. Specifically, we were interested in (1) the level of research interest in enrichment in recent years, using papers published per year on this topic as a proxy; (2) research interest at a species level for a selection of laboratory and aquaculture species; and (3) an overview of the range and frequency of parameters used to quantify welfare. These surveys were performed in Web of Science (Core Collection) on 03/06/2024. Search terms used are listed in Appendix S1.

3 | Current Status Quo of Environmental Enrichment Research in Fishes

Although the last two decades have seen growth in research on enrichment, the overall percentage of papers focused on enrichment has not matched the general rate of increase in fish welfare papers (Figure 1b), and large gaps remain. Across species, research into welfare and enrichment is not evenly distributed. Within both aquaculture species and those used primarily as models for laboratory research, species that are overall less common are, unsurprisingly, also less well-understood in respect to their welfare—with a general trend of a lower percentage of welfare-related papers for species with fewer overall papers published (Figure 2a; Spearman's rank correlation, $S=55{,}033$, $p=0.015$, $\gamma=0.277$). Within enrichment research specifically, however, this trend is stronger. Even highly studied aquaculture species show relatively low levels of enrichment-specific research (Spearman's Rank correlation, $S=3942$, $p=0.052$, $\gamma=0.341$) with a similar relationship for 'pure' research species (Figure 2b; Spearman's rank correlation, $S=6232.1$, $p<0.001$, $\gamma=0.561$). Even within the better-studied species, the provision of enrichment can lead to contradictory outcomes. The conflicting outcomes across studies and types of enrichment are well summarised by two recent and comprehensive reviews (Lee, Paull, and Tyler 2022; Stevens, Reed, and Hawkins 2021). In salmonids, similarly, enrichment can have significant effects, but depending on what and when enrichment is provided these effects can vary from beneficial—such as improved growth rates (Finstad et al. 2007) and physiological measures (Millidine, Armstrong, and Metcalfe 2006) in the presence of shelter—to negative, such as decreased growth rates and lower post-release survival in smolt (Rosengren et al. 2016; Solås, Skoglund, and Salvanes 2019).

The metrics used to determine optimal enrichment conditions often vary between studies (Figure 3). Research into husbandry, welfare and enrichment is typically conducted with the aim of determining optimal growth and survival, reproductive output, and/or minimising physical or behavioural indicators of stress. Growth, as a relatively simple-to-assess metric with generally clear interpretation and particular relevance to aquaculture, is the most commonly studied aspect of welfare and enrichment studies in fishes. Behavioural metrics (including activity rates, swimming patterns, avoidance/attraction responses, space and shelter use, shoaling patterns, feeding behaviour and aggression (Huntingford et al. 2006)) are also common in welfare studies (Beitinger and McCauley 1990) as metrics that can be assessed in relatively short timescales and that may be sensitive to early or small changes in conditions. Mortality and incidence of pathologies such as diseases, lesions, injuries or parasites, alongside morphological abnormalities, are also used (Huntingford et al. 2006; Ellis et al. 2012), but may not be reliable indicators of some kinds of stress or in some species (Noga 2000; Davis and Ottmar 2006). Physiological or gene-expression changes such as alterations in ventilation rates, composition of blood and plasma (gases, hormones such as cortisol, or ions), immune response and production of heat shock proteins may provide more reliable indicators of (acute or chronic) stress, but are often impractical or resource-intensive to measure, vary between species and may not map well to long-term effects or health (Huntingford et al. 2006; Barton 2002). While it is not unusual for studies to use multiple welfare metrics, for example, growth and mortality, relatively few explicitly examine the relationships between them—particularly links between short-term responses and long-term outcomes are scarce (Huntingford et al. 2006). However, this is beginning to change: Davis (2010) examined

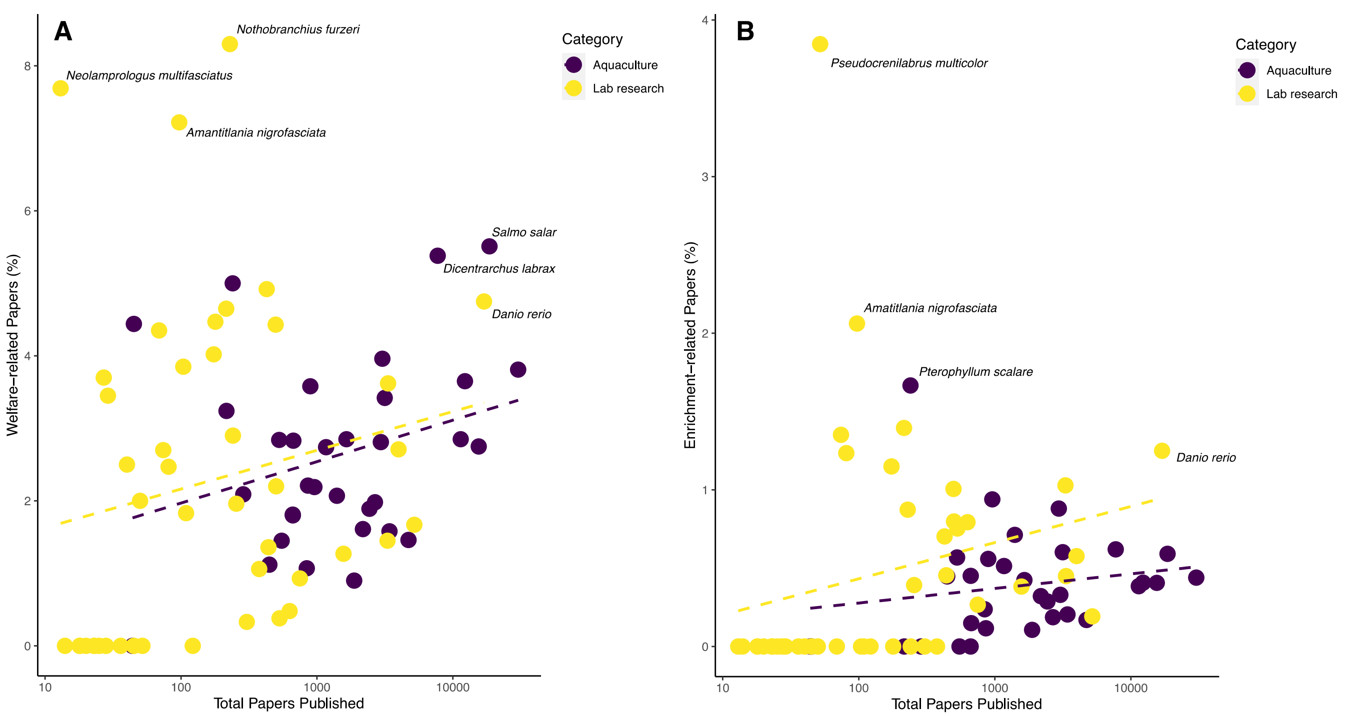

FIGURE 2 | (A) the percentage of papers relating to welfare for a species increases with the total number of published papers concerning the species; each point represents one species, with outlying species named. For enrichment-specific papers (B), this trend holds for laboratory species but is weaker for aquaculture species. Species are assigned a category as 'aquaculture' or 'lab research' depending on their most common topic classification on Web of Science. Note logarithmic scales on x-axes.

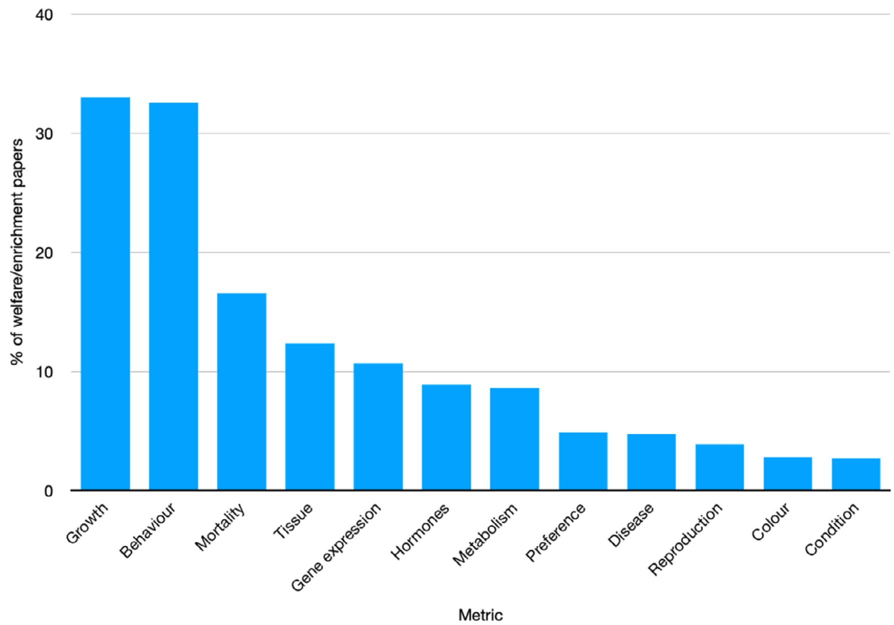

FIGURE 3 | Incidence of various metrics of welfare within papers studying fish welfare/enrichment. Metrics are not mutually exclusive; studies may simultaneously record multiple metrics. See Appendix S1 for search terms used.

links between behavioural reflex impairment and mortality; Anders et al. (2022) correlated physiological, neuro-endocrine and physical stress responses with behavioural metrics during swimming and handling; and Georgopoulou, Vouidaskis, and Papandroulakis (2024) assessed the relationship between behavioural indicators and feeding rates in European seabass (*Dicentrarchus labrax*).

There are many aspects of physical enrichment that may affect fish welfare and behaviour, some of which have received more attention than others. Substrate preferences have historically been a key focus of enrichment studies (Näslund and Johnsson 2016; Maia, Saraiva, and Gonçalves-de-Freitas 2024). Much of the early work on substrate preferences in fishes was observations made while encouraging and enabling more 'natural' behaviours in ecological experiments (Kalleberg 1958; Meuthen et al. 2011). Later work was conducted from a behavioural ecology perspective, such as Hart's work on habitat preferences and foraging efficiencies in three-spined sticklebacks (*Gasterosteus aculeatus*) (Hart 2003; Webster and Hart 2004, 2006).

The provision of shelter for captive fishes has been another early focus of work on welfare, for example as a factor affecting growth and reducing resting metabolism in salmonid fishes (Benhaïm, Leblanc, and Lucas 2009; Finstad et al. 2007; Millidine, Armstrong, and Metcalfe 2006; Näslund et al. 2013; Valdimarsson and Metcalfe 1998). Laboratory and captive work has been complemented by ecological studies in the wild exploring structural complexity and habitat niches (Harding, Burky, and Way 1998; Kerry and Bellwood 2012; Kessel et al. 2011; Khan et al. 2017; Love et al. 2006; Ménard et al. 2012), as well as specific functions of shelters such as large corals which were shown to be used as shade from UV-B irradiance in large reef fishes (Kerry and Bellwood 2015). Research suggests that, alongside such specific functional contexts, physiological benefits derived from presence of shelter are likely to be also influenced by the size of the fish, size of shelter and social context (Chrétien, Cooke, and Boisclair 2021).

Researchers are now investigating an increasing number of aspects of physical enrichment and exploring alternative forms of potential enrichment. There is growing interest on the provision of areas with water flow (Villalba et al. 2024; DePasquale et al. 2019) and the associated effects of exercise on multiple welfare parameters (Guo et al. 2024). Work trying to find the most practical and convenient forms of enrichment is focusing on additions that reduce cleaning and maintenance costs while providing physical enrichment, such as research examining the effects of objects suspended from tank lids (Crank, Kientz, and Barnes 2019; Kientz and Barnes 2016; Voorhees et al. 2020; White et al. 2019) or bubble curtains (Amichaud et al. 2024). Researchers have also explored potential benefits of more active methods of improving welfare, such as testing impacts of frequent water changes on welfare of zebrafish (Lee, Tyler, and Paull 2018) or angelfish (*Pterophyllum scalare*; Gauy, Boscolo, and Gonçalves-de-Freitas 2018), or providing active stimulus for predatory fishes, as in the case of laser pointers used as visual stimuli to encourage arapaima (*Arapaima gigas*) to move and explore within their housing tanks (Matrai et al. 2023). There is also exploration of the effects of physical forms of cognitive enrichment (see review by (Kleiber et al. 2023)), such as provision of 'puzzle feeder' challenges (Varracchio et al. 2024).

Another area in which enrichment research is expanding is the range and type of tests which are done to determine the effects of a given enrichment. Classically, enrichment studies have often involved relatively simple presence/absence comparisons, typically testing the effect of a particular type of enrichment against a barren tank (Fabre et al. 2020). Recently, however, studies have begun to move beyond dichotomous preference tests to investigate the effect of a range of options, including colours, types, amounts and dimensions of enrichment (Lavery and Mason 2023; Josi, Taborsky, and Frommen 2018; Jones, Gardella, and Webster 2024; Wu et al. 2020; Zhang et al. 2019). The possibility of optimum levels beyond which enrichment becomes less effective or even negative is also being explored (e.g., (Ruberto, Swaney, and Reddon 2024)). More attention is also now being paid to the context and background of fish tested, such as comparisons between effects of enrichment on different ages of fishes (Fazekas et al. 2023; Green and Swaney 2023), or examination of the effects of length of exposure to enrichment (Iffert and Stein 2024).

Beyond improving research validity, there is a growing number of studies exploring applications for enrichment in conservation. Examples include the captive husbandry of threatened or endangered species, like the near-threatened (*Schizothorax wangchiachii*; Wu et al. 2020; Zhang, Fu, et al. 2022), and the effects of enrichment on reproductive success in the endangered redside dace (*Clinostomus elongatus*; Watt, Mokdad, and Pitcher 2024). Knowledge of the effects of enrichment on fish in captivity may also allow more effective conservation measures in situ: identification of important environmental aspects for species survival can allow for targeted protection or restoration of habitat. For example, endangered Knysna seahorses (*Hippocampus capensis*) have been shown to prefer artificial structures introduced into their environment over 'natural' seagrass habitat (Claassens 2016), with this preference suggested to be driven by an increased availability of holdfasts, shelter and food availability by the artificial structure (Claassens, Booth, and Hodgson 2018). Additionally, manipulation of enrichment may be utilised to alter species' behaviour in beneficial ways—for example, Li et al. (2022) explored how preferences for specific substrates and artificial light may be harnessed to improve utilisation of fish passageways. For hatcheries focused on releasing fish back into the wild, the use of enrichment to influence learning of critical survival skills can be hugely important—for example, post-release foraging skills can be improved by enrichment (Brown and Laland 2002; Magnhagen and Staffan 2003; Reid, Seebacher, and Ward 2010). Similarly, rearing fish in structurally enriched environments can help improve the behavioural response to risk and enhance survival of young fishes after release (Roberts, Taylor, and Garcia de Leaniz 2011).

4 | Future Outlook and Suggestions

Although 'more!' is the classic cry of any researcher within a topic, it is worth considering the most fruitful directions research can take, and the factors which stymie such studies. As we have shown, increased research effort in recent years may still often be focused on specific species and questions, rather than examining general trends. Analysis of a broader variety of species, as well as a broader variety of enrichment types, will allow identification such trends across taxa and/or patterns of traits that are predictive of enrichment preferences. These may facilitate better prediction of requirements for harder-to-study species, including endangered species which may not be possible to study directly. Similarly, exploration of the relationships between welfare metrics (e.g., links between short- and long-term metrics of welfare) may allow development of more efficient ways to assess welfare.

What stands in the way of developing this research? Simply put, a large factor is that welfare studies of fishes may have been perceived as relatively low-impact, and of low academic value. As a consequence, they tend to be published in journals with comparatively low-impact factors (cf. Goulart et al. 2009), making them less attractive for many funders. The species-specific nature of welfare requirements in fishes means that such studies are likely to be cited chiefly (and perhaps only) by researchers who work on that species, rather than the discipline as a whole. This is a possible reason that there is a positive relationship between the number of papers about a species and the percentage of papers concerning the welfare/enrichment of that species, particularly within those used as laboratory models: for rarely studied species, there is a smaller 'market' and therefore less incentive. Furthermore, while 'methods' papers are commonly cited as shorthand ways to reduce a methods section, it may be rare to cite welfare papers to justify husbandry choices even when they did inform protocols. Indeed, while there is no quantitative study of citations of welfare papers used to inform husbandry, Jones, Webster, and Salvanes (2021) showed that even papers specifically focused on welfare rarely provided rationale for the use of enrichment, whether that was pilot studies or citations of previous work. Additionally, welfare studies may be resource-intensive, either in terms of equipment and reagents required, or in terms of time (particularly for long-term or growth studies). For groups using model species to study specific questions, even running a husbandry welfare study 'in the background' may be problematic, as it adds complicative factors which have the potential to affect results.

How can these barriers be overcome? Both top-down and bottom-up approaches may be effective in incentivising welfare and enrichment research. Provision of specific funding and grants to support such research may encourage development of studies and allow the freedom to pursue them as a main focus. On the researchers' side, normalising citation of welfare studies as part of research (e.g., to justify husbandry protocols) may increase the average impact of welfare papers, and hence the attractiveness of publishing them. The latter suggestion intersects with another aspect of developing welfare research: in recent years, there has been a push towards improving reporting of housing conditions as part of publication of studies, such as use of the DETAILS framework (Jones, Webster, and Salvanes 2021), the development of The FishEthoBase, a global assessment of welfare in farmed fishes (Saraiva et al. 2019) and public sharing of laboratory protocols (e.g., protocols.io). Inclusion of details such as the enrichment, social conditions, lighting, and water parameters of housing for fish used in experiments may allow identification of crucial differences which may explain discrepancies between study results. In addition, standardised reporting may facilitate meta-analyses examining impacts of welfare or best-practice techniques on a broad scale.

Alongside standardised reporting of husbandry techniques, standardised protocols for assessing and testing impacts of enrichment or other aspects of welfare may also facilitate 'quick and easy' studies with cross-species applications. These may be particularly valuable as student projects: standardised welfare studies have the potential to be relatively (narratively and technically) simple, straightforward and low-risk—with a solid chance for a publication which may be valuable at the start of a researcher's career regardless of its impact factor.

Attention to welfare and husbandry techniques of captive fishes—including enrichment—is increasing, driven by increasing interest in welfare in fisheries (Ashley 2007; Browman et al. 2018; Bui et al. 2019; Kleiber et al. 2023; Turnbull and Huntingford 2012; Williams, Readman, and Owen 2009) and the ornamental trade (Jones et al. 2022, 2023; Saxby et al. 2010; Vanderzwalmen et al. 2020, 2022). Papers focusing on enrichment and welfare are growing in frequency and in scope, with researchers exploring multiple potential avenues to improve welfare through enrichment. There are also calls for studies across a greater variety of species, including those which are relatively less studied. Researchers are beginning to expand investigations of the methods and applications of welfare/enrichment research, with more attention paid to the metrics and testing techniques used. Alongside increasing recognition of the importance of standardised (or at least explicitly reported) husbandry protocols across research, applications of enrichment research beyond welfare considerations (such as use of enrichment to influence behaviour) are emerging. As the importance of captive fishes in research, aquaculture and conservation continues to increase, so too must our knowledge of the most effective, and efficient, ways to enrich their housing.

Author Contributions

Conceptualisation: H.C.S.-J., J.G.F. and N.A.R.J. Methodology: H.C.S.-J. and N.A.R.J. Investigation: H.C.S.-J. Writing (original draft): H.C.S.-J. and N.A.R.J. Writing – Review: J.G.F. Revising: H.C.S.-J., J.G.F. and N.A.R.J. Visualisation: H.C.S.-J. Project administration: N.A.R.J.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data collected in the survey are available in Appendix S1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.