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Behavioural Diversity of Fishes: Concepts, Drivers and Its Role in Conservation and Management

Marie Prchalová[1] | Robert Arlinghaus[2,3] | Samuel Westrelin[4] | Ivan Jarić[1,5] | Michael G. Bertram[6,7,8] | Josep Alós[9] | Henrik Baktoft[10] | Jack A. Brand[6,11] | Tomas Brodin[6] | Adolfo Cordero-Rivera[12] | Carlina Feldmann[13] | Ryo Futamura[2,14] | Stefan Hont[15] | Pascal Klamser[16] | Cecilie Iden Nilsen[17,18] | Johann Mourier[19] | Karl Øystein Gjelland[20] | Esben Moland Olsen[21] | Polona Pengal[22] | Rubén Rabaneda-Bueno[1] | Milan Říha[1] | Theresa Rueger[23] | Holger Schielzeth[24] | Marco Signaroli[9] | Marija Smederevac-Lalić[25] | Christopher T. Monk[26]

[1]Biology Centre of the Czech Academy of Sciences, Institute of Hydrobiology, České Budějovice, Czech Republic | [2]Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany | [3]Division of Integrative Fisheries Management, Faculty of Life Sciences and Integrative Research Institute on Transformations of Human-Environment Systems (IRI THESys), Humboldt-Universität zu Berlin, Berlin, Germany | [4]INRAE, Aix Marseille Univ, RECOVER, Aix-en-Provence, France | [5]CNRS, AgroParisTech, Ecologie Systématique Evolution, Université Paris-Saclay, Gif-sur-Yvette, France | [6]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden | [7]Department of Zoology, Stockholm University, Stockholm, Sweden | [8]School of Biological Sciences, Monash University, Melbourne, Australia | [9]Department of Marine Ecology, Instituto Mediterráneo de Estudios Avanzados, IMEDEA (CSIC-UIB), Esporles, Spain | [10]DTU Aqua, Section for Freshwater Fisheries and Ecology, Silkeborg, Denmark | [11]Institute of Zoology, Zoological Society of London, London, UK | [12]Universidade de Vigo, Pontevedra, Spain | [13]Statistics and Data Analysis Group, Faculty of Business Administration and Economics, Bielefeld University, Bielefeld, Germany | [14]Atmosphere and Ocean Research Institute, The University of Tokyo, Kashiwa, Chiba, Japan | [15]Danube Delta National Institute for Research and Development, Tulcea, CP, Romania | [16]Center Synergy of Systems & Center for Interdisciplinary Digital Sciences, TUD Dresden University of Technology, Dresden, Germany | [17]Department of Biological Science, University of Bergen, Bergen, Norway | [18]NORCE Norwegian Research Centre, LFI Laboratory for Freshwater Ecology and Inland Fisheries, Bergen, Norway | [19]MARBEC, Univ Montpellier, CNRS, IFREMER, IRD, Sète, France | [20]Norwegian Institute for Nature Research, Tromsø, Norway | [21]IMR, Institute of Marine Research, Flødevigen Marine Research Station, His, Norway | [22]Institute for Ichthyological and Ecological Research, REVIVO, Dob, Slovenia | [23]Dove Marine Laboratory, School of Natural and Environmental Sciences, Newcastle University, Newcastle-upon-Tyne, UK | [24]Institute of Biodiversity, Ecology and Evolution, Friedrich Schiller University Jena, Jena, Germany | [25]University of Belgrade - Institute of Multidisciplinary Research Kneza, National Institute of the Republic of Serbia, Belgrade, Serbia | [26]Marine Ecology, GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

Correspondence: Christopher T. Monk (cmonk@geomar.de)

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ABSTRACT

Human activity has altered nearly all ecosystems on Earth, contributing to substantial biodiversity loss across taxonomic, genetic and functional dimensions, from the intraspecific to the ecosystem scale. Yet some components of biodiversity remain hidden or underappreciated, including behavioural diversity. Behaviour is often among the earliest whole-organism responses to environmental change, and diversity in behaviour can occur within individuals, among individuals, among populations and across communities and ecosystems. This variation may influence growth, survival, reproduction, ecological interactions and responses to anthropogenic pressures, although its effects on population stability and resilience are likely context-, scale- and component-dependent. In this review, we examine behavioural diversity in fishes, defined here as variation in behavioural traits across levels of biological organisation, from individuals to ecosystems. Our review has two complementary aims. First, we provide a conceptual overview of behavioural diversity, clarify how it differs from related constructs such as personality, plasticity, and behavioural syndromes, and summarise the evolutionary, ontogenetic, ecological, stochastic and anthropogenic processes that

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generate or erode it. Second, we evaluate why behavioural diversity matters for fish ecology, fisheries management, aquaculture, restoration and conservation. We conclude by identifying key research needs, including improved quantification, stronger empirical links between behavioural diversity and ecological outcomes, and the development of management approaches sensitive to behavioural diversity. More explicit consideration of behavioural diversity should improve our ability to predict fish behavioural diversity responses and to design conservation and management measures that account for variation rather than only average behavioural responses.

1 | Introduction

In the face of the Earth's sixth mass extinction, biodiversity conservation is vital (Barnosky et al. 2011; Caro and Sherman 2012). Biodiversity commonly includes taxonomic, genetic and functional diversity, spanning intraspecific to ecosystem levels (Cadotte et al. 2011; Flynn et al. 2011). Other components of biodiversity have remained hidden and unrecognised (Des Roches et al. 2021), including behavioural diversity (Caro and Sherman 2012; Cordero-Rivera 2017). However, behaviour constitutes a key level of biodiversity that moderates the complex interactions of organisms with their biotic and abiotic environments (Pollock et al. 2020). Importantly, behaviour is not only a component of biodiversity and multiple ecological processes, but also plays a central role in shaping evolutionary processes, such as adaptive radiations (Sommer-Trembo et al. 2024) and life-history evolution (Wolf and Weissing 2012) including life-history endpoints such as age at death (Bedbrook et al. 2026).

Behaviour is often the first of a series of responses to a change in environmental conditions (Sih 2013). Behavioural diversity may influence how individuals and populations respond to environmental change, but its effects on resilience and stability are likely context-, scale- and component-dependent. Behavioural diversity should therefore be considered a potentially important, but still insufficiently resolved, component of biodiversity in contemporary conservation management (Rota et al. 2025; Wong et al. 2024). The diversity of behaviours observed across organisms in nature is vast. Recognising this, Cordero-Rivera (2017) advocated for a new level of biodiversity, which he termed 'ethodiversity'—'etho-' derived from ethology, the comparative study of animal behaviour. He defined ethodiversity as the variation in behavioural traits at the individual (e.g., personality), population (e.g., alternative reproductive strategies), community and ecosystem levels (e.g., contrasting behavioural patterns between species and variation in the behaviour of the same species in different ecosystems). Considering that ethology primarily refers to the study of individual organism behaviour, behavioural diversity as a broader concept may better reflect the diversity of population-specific variation in behavioural phenotypes, repertoires and traits. We, therefore, propose the term 'behavioural diversity', rather than ethodiversity, to capture all facets of behavioural variation exhibited by individuals, populations, and communities of organisms in different ecosystems.

Preserving behavioural diversity is expected to be central to ensure the stability and resilience of populations, and to understand how individuals and populations collectively respond to a rapidly changing environment (Candolin and Rahman 2023; Shumway 1999). Current biodiversity prediction tools, however, often treat species as groups of individuals with uniform behaviours (e.g., thermal sensitivity to climate change; Bellard et al. 2022). Yet individuals within populations and species show structured behavioural variation that may not be well captured by population averages (Bolnick et al. 2011) and may be better described by variances (Jeltsch et al. 2013; Keith et al. 2023; Sanmartín-Villar and Cordero-Rivera 2024). In addition, populations and species may exhibit collective cultural properties and, in some cases, also include socially transmitted behavioural traditions (Brown and Webster 2025). A better understanding and representation of behavioural diversity will improve our ability to predict biodiversity responses and inform where conservation measures are likely to be most effective (Marske et al. 2023), especially in times of rapid global change (Fredston et al. 2025; Jeltsch et al. 2025).

Behavioural diversity has received less attention than other levels of biodiversity for several reasons. Contributing factors include a long-standing reliance on average phenotypes (Krebs and Davies 2009), ongoing debate over how behaviour should be defined and measured (Levitis et al. 2009), and until recently, limited tools for quantifying behaviour in the wild (Berger-Tal et al. 2025; Nathan et al. 2022). Research bias is also intensified when experimental studies focus on a small number of model species (Webster and Rutz 2020), use domesticated or captive-bred individuals, or employ rearing conditions that differ substantially from those in the wild, such as unnaturally high densities, unlimited food or lack of predators. These conditions can lead to behavioural changes, reduced behavioural variation and lower responsiveness (Bubac et al. 2020).

Here, we examine behavioural diversity in fishes as an underappreciated dimension of biodiversity (Figure 1). Fishes represent roughly half of vertebrate diversity (Froese and Pauly 2024; Nelson et al. 2016), exhibit extensive behavioural variation across ecological contexts (Fernö et al. 2020; Meager et al. 2018), provide important ecosystem services (Holmlund and Hammer 1999; Lynch et al. 2016), and are managed in fisheries and conservation (Arlinghaus et al. 2013; Arthington et al. 2016). Recent reviews have shown that behavioural ecology can improve fish conservation and management by linking concrete management questions to theory and methods concerning diet choice, patch use, habitat selection, movement, and social behaviour (Malone and Polivka 2022). In fisheries, the behavioural dimension remains the most elusive, as many unexpected outcomes of well-intentioned management measures can be attributed to unforeseen behavioural processes (Pine III et al. 2009).

This review has two complementary aims (Figure 2): first, to introduce behavioural diversity conceptually and outline how it arises across hierarchical levels; and second, to evaluate its

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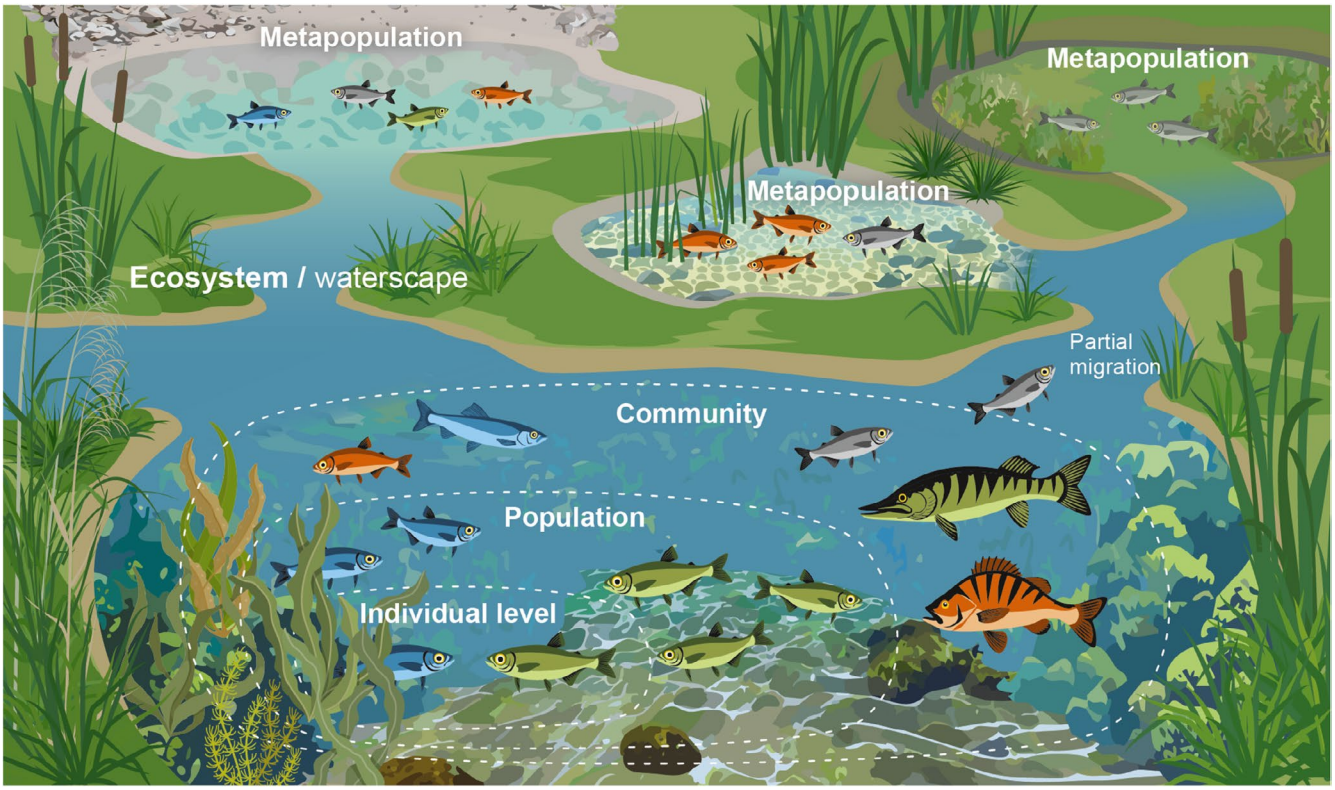

FIGURE 1 | Illustration of how fish behavioural diversity is present at every level of biological organisation of biodiversity, from the individual animal to metapopulations and variation at the ecosystem level. Different behaviours within a species are depicted using different colours for individuals. Partial migration is shown as an example of a process inducing behavioural diversity, resulting in different behavioural repertoires in connected ecosystems and metapopulations.

relevance to fish ecology and its implications for management and conservation. Methodological and technological advances relevant to quantifying and studying behavioural diversity are summarised in the Supporting Information. Rather than offering an operational management toolkit (Malone and Polivka 2022), our aim is to frame behavioural diversity as a biodiversity dimension that should be explicitly considered in applied fisheries science and fish conservation.

2 | Behavioural Diversity as a New Biodiversity Level

2.1 | Behavioural Expressions—The Units of Behavioural Diversity

Behaviours are typically considered internally coordinated responses (actions or inactions) of whole living organisms, whether individuals or groups, to internal or external stimuli, excluding responses better understood as developmental changes (Levitis et al. 2009). At any given moment, an observed behaviour, or behavioural expression, can be viewed as the outcome of an organism's internal state, its capacity to behave and the prevailing biotic and abiotic environment (Figure 3a) (Nathan et al. 2008). Internal state includes physiological and psychological conditions that shape motivation, whereas behavioural capacity includes the physical, sensory and cognitive abilities that enable action. State-dependent behavioural expression is especially clear in antipredator contexts, where optimal risk-taking can depend on condition, reproductive value, and the assets an individual has to protect (Clark 1994). Behaviour may therefore be driven not only by cognition, but also by physiological, reflexive or instinctual processes, and can also be modified indirectly through environmental effects on physiology. Such environmentally induced physiological effects can include epigenetic pathways that influence social behaviour (Seebacher and Krause 2019) and may contribute to later-life variation in migration tendency and timing through early-environment effects (Jonsson and Jonsson 2014) or interact with foraging behaviour and trophic morphology (Adams et al. 2003). Epigenetics is therefore treated not as a separate behavioural level, but as one pathway through which developmental history and environmental exposure can shape behavioural expression later in life (represented in Figure 3a by the arrows linking external factors to internal state and behavioural expression). Behavioural diversity arises from a diversity of behavioural expressions.

Behavioural variation is known to be highly structured (Figure 3b) (Laskowski, Chang, et al. 2022). Statistical approaches to repeatability and variance partitioning show that behavioural variation can be decomposed into among-individual differences, within-individual plasticity, and differences in predictability or residual variability (Nakagawa and Schielzeth 2010; O'Dea et al. 2022). Personality refers to consistent among-individual differences in average behaviour, plasticity to within-individual behavioural change across contexts or gradients, predictability to among-individual differences in within-individual residual variation and behavioural syndromes to correlations among behavioural traits

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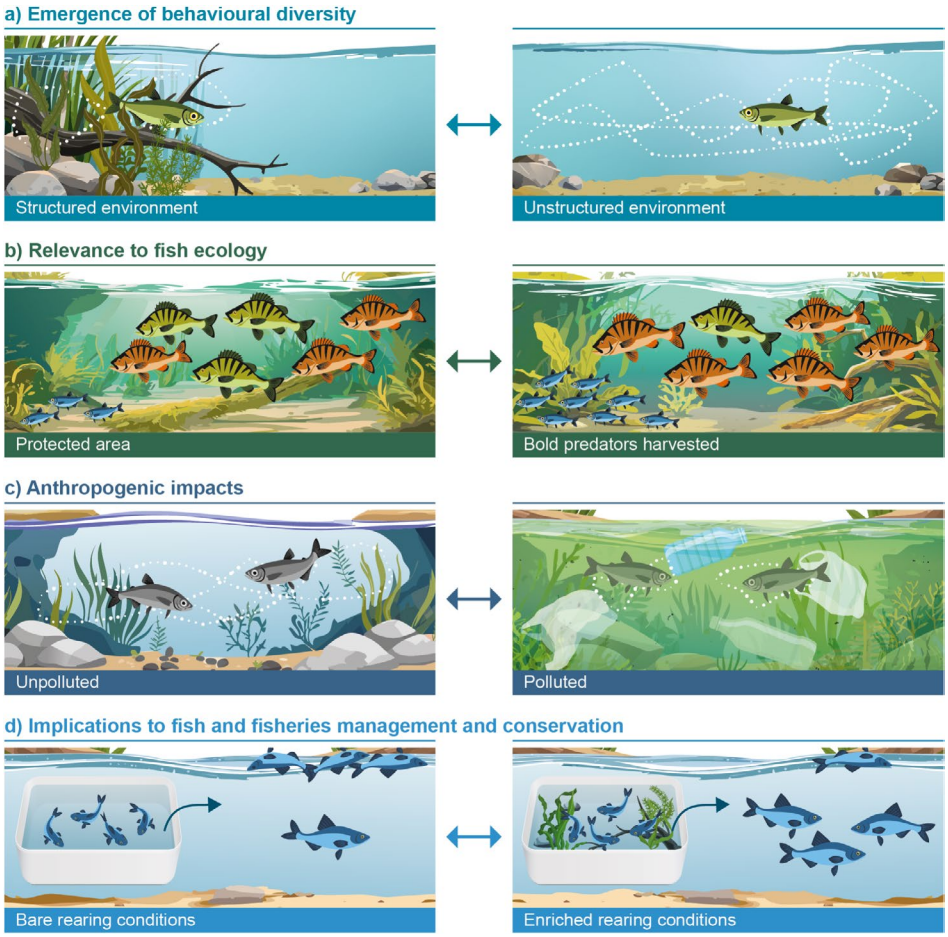

FIGURE 2 | Illustrative examples related to behavioural diversity, corresponding to the main themes of the review. (a) Emergence of behavioural diversity (increased space use and swimming activity in an unstructured environment). (b) Relevance to fish ecology (decreased predation and increased prey abundance in a harvested population, where predator abundance is unchanged, but the behavioural composition changes). (c) Anthropogenic impacts (swimming activity affected in polluted waters). (d) Implications for fish and fisheries management and conservation (increased survival of fish reared in enriched conditions). Inspiration taken from Kobler et al. (2009) and Říha et al. (2021) for plot a, plot b from Rhoades et al. (2019), plot c from Polverino et al. (2021) and plot d from Hyvärinen and Rodewald (2013).

(Dingemanse et al. 2010; Sih, Bell, and Johnson 2004). These constructs describe different components of behavioural variation, but none is synonymous with behavioural diversity. Behavioural diversity, as used here, is broader and refers to the distribution and structure of behavioural expression across individuals, contexts, groups, populations and higher levels of biological organisation. Because these variance components may change across time and contexts, and can covary with one another, behavioural diversity, like biodiversity more broadly, is a meta-concept that cannot be fully captured by any single indicator or reduced to a single component (Laskowski, Chang, et al. 2022; Winter and Schielzeth 2025).

Behaviour is further organised hierarchically across spatio-temporal scales (Figure 3c), because broader patterns are composed of lower-level acts (Henderson 1990; Réale et al. 2007). For example, foraging may include searching, attacking, handling, consuming and moving among feeding sites while avoiding predators. Microscale processes thus scale up to broader behavioural patterns that shape growth, survival, reproduction, population dynamics and ecosystem services (Nathan et al. 2008). This hierarchical and feedback-rich nature of behaviour makes behavioural diversity inherently multi-layered and context dependent (Dingemanse et al. 2007). It also supports linking behavioural diversity to biodiversity dynamics more broadly, because movement and behaviour can connect resources, genes and processes across habitats and mediate coexistence through equalising and stabilising mechanisms (Jeltsch et al. 2013, 2025).

2.2 | Biodiversity Framework Integration

The full range of behavioural expression can be quantified as behavioural diversity when the level of organisation, behavioural variables, context and temporal window are explicitly defined. Behaviours, or expressions of behavioural variables, can be treated as units of behavioural diversity and discrete behavioural repertoires can be summarised using standard diversity metrics such as richness, evenness, Simpson's index, Shannon diversity or alpha, beta and gamma diversity (Pielou 1966). For continuous traits and hierarchical behavioural variation, however, mixed-effects models, reaction norms, variance partitioning and multivariate trait-based approaches will often be

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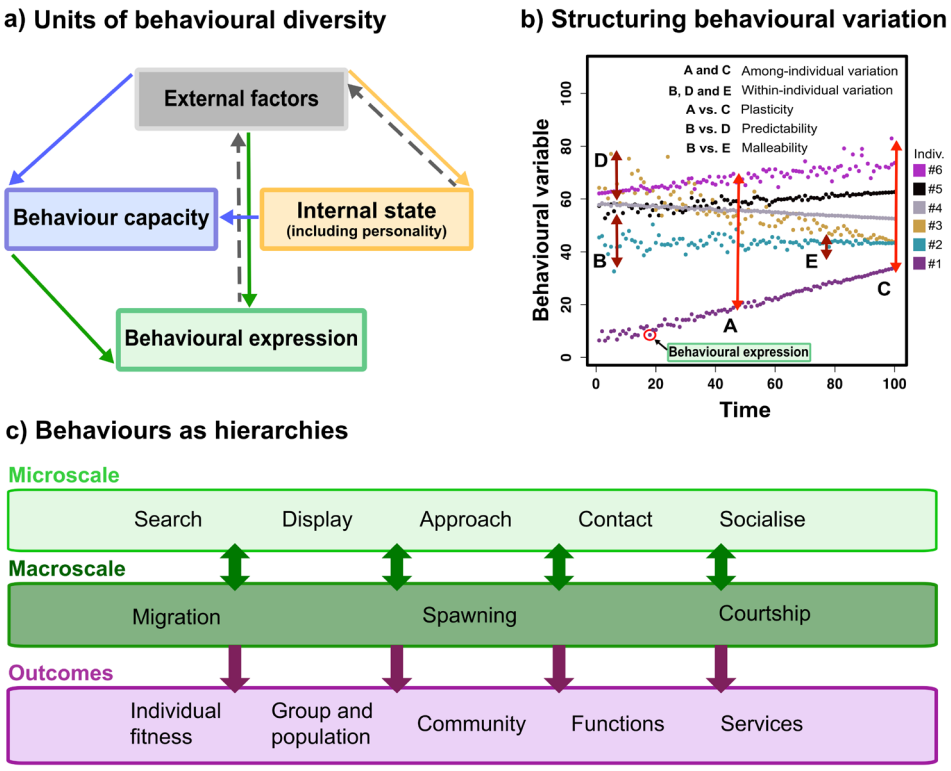

FIGURE 3 | Diagram illustrating (a) how behaviour is generated, (b) how behavioural variation is structured and (c) how behaviours relate across different spatio-temporal scales, from actual behavioural processes through higher levels of displays in the context of mating, to general outcomes ranging from individual fitness to ecosystem services. Each level does not contain an exhaustive list of examples. Arrows represent links between processes and behaviours, but not all possible relationships are captured.

more appropriate than simple categorical indices (Cronin and Ross 2019; Dingemanse et al. 2010).

Once behaviour is quantified, behavioural diversity can be compared among individuals, groups, populations or communities using approaches adapted from functional diversity, including dissimilarity matrices, functional dendrograms and multidimensional spaces such as binary or probabilistic hypervolumes (Mammola et al. 2021; Schleuter et al. 2010). These approaches can describe behavioural richness, divergence and regularity, but no single metric can capture behavioural variation across all hierarchical levels simultaneously.

Quantification also helps distinguish among components of behavioural variation, including among-individual differences, within-individual plasticity, predictability and behavioural syndromes (Dingemanse et al. 2010; O'Dea et al. 2022). Because within-individual variation is common, including repeated individual variation in migration timing in migratory fishes (Jensen et al. 2020), behavioural diversity should ideally be assessed through repeated measurements at the individual level. Failing to account for within-individual variation in behavioural expression would likely underestimate behavioural diversity (Palacio et al. 2019) and collapse important variation into population averages.

One important step is to begin aggregating behavioural measures in curated trait databases. Recent movement-trait approaches illustrate one tractable route for operationalising selected components of behavioural diversity: repeated individual-level biologging data can be converted into standardised movement traits, while retaining information on species-level, among-individual, and within-individual variation (Beumer et al. 2026). For fishes, analogous telemetry, biologging, video and sonar-based workflows could help quantify movement-related components of behavioural diversity (Beumer et al. 2026). The development of such standard databases will also support decision making in how to split or lump behaviours across the hierarchy, which is a critical challenge in many studies of behavioural variation (Cronin and Ross 2019).

Cordero-Rivera (2017) outlined why behavioural diversity is distinct from functional diversity: a single outcome can result from multiple alternative behaviours, many behaviours may not be directly associated with a functional role and most studies of functional diversity examine only a limited set of traits. Therefore, behavioural diversity as a biodiversity level may have unique features relative to other biodiversity concepts. The first feature is that non-evolutionary processes, such as learning, may be especially important for generating novel diversity relative to other biodiversity levels. Behaviour can be transmitted across generations culturally (Whiten 2017), and within a generation, behaviours may spread via social learning processes (Brown and Laland 2003). The second feature is that behavioural diversity can only be measured over a set time duration and cannot be assessed from a single snapshot. The full intensity of a behavioural expression cannot be quantified until the behaviour is finished, and therefore behavioural measurements always require a range of time under consideration, which is a critical challenge for empiricists. A third feature is that traces of

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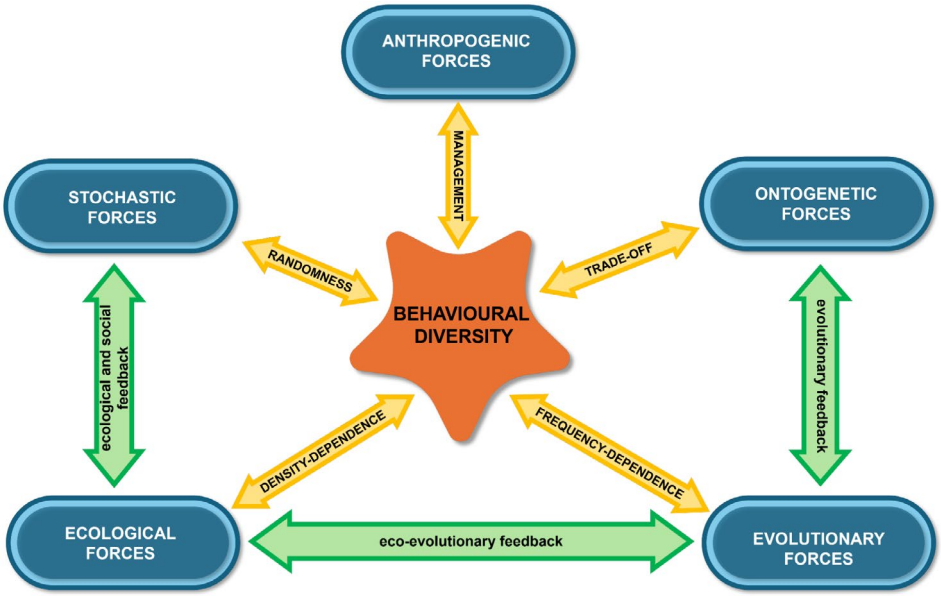

FIGURE 4 | Conceptual diagram of the factors that shape behavioural diversity. Four key natural pathways and the anthropogenic influences that affect or shape behavioural diversity are in blue. Green arrows indicate key feedback processes. Yellow arrows denote key ecological mechanisms and processes that, in isolation or through feedback loops, can give rise to behavioural diversity (or erode it). This framework is consistent with the original Tinbergen's levels of explanation for traits (*sensu* any measurable aspect of biology) (Tinbergen 1963) where we should ask how traits function, how they influence fitness and how they develop through ontogeny and evolution (Endler 2025).

behaviour are ephemeral, which makes it difficult to infer behaviours after their expression. Tools such as biotelemetry are promising candidates to infer behaviours of fishes in the wild (Beumer et al. 2026; Nathan et al. 2022), and in the laboratory novel technology is allowing full enumeration of behaviours, in some cases across the whole animal life (Bedbrook et al. 2026). That said, important limitations remain as certain behaviours such as vocalisation or communication are challenging to quantify, especially in fishes (Yllan and Rueger 2025).

3 | How Behavioural Diversity in Fishes Arises

Behavioural diversity arises through interactions among internal state, behavioural capacity, and external conditions (Figure 3a), and is shaped by evolutionary, ontogenetic, ecological, stochastic and anthropogenic forces (Figure 4). Notably, anthropogenic forces occur because human activities can modify each of the other pathways and may impose selective pressures that differ from many natural drivers, for example through fisheries-induced selection on behaviour (Monk et al. 2021). These categories are therefore heuristic rather than mutually exclusive, but they help organise the main processes that generate behavioural diversity and provide a clearer transition to the next section.

3.1 | Evolutionary Forces

Across generations, behavioural diversity is shaped by selection, gene flow, mutation and genetic drift. Behavioural traits often show heritable variation comparable to that of morphological and life-history traits, although heritability differs among behaviours and can be especially high for migration-related traits (Dochtermann et al. 2019). Furthermore, behaviour often stems from polygenic architecture, slowing adaptive change compared to traits with fewer governing genes (Bubac et al. 2020; Laine and van Oers 2017). However, instances of single genes determining behaviours, such as migration timing, have also been identified (Niemelä et al. 2022).

Direct selection acts when behavioural traits themselves affect fitness (e.g., spawning timing in salmonids; Crozier et al. 2020), whereas fluctuating selection can maintain variation when the fitness consequences of behaviour change across environments, life stages, or social contexts (Smith and Blumstein 2010). Activity, for example, may increase foraging gains but also predation risk (Monk et al. 2021), and the same behavioural tendency may reduce survival when fish are small but increase survival or reproductive output later in life (Ballew et al. 2017; Moiron et al. 2020). Behavioural variation can also persist through balancing selection, especially in discrete polymorphisms and alternative reproductive tactics, where rare tactics may gain a fitness advantage when uncommon, preventing fixation of a single strategy (Brisson 2018; Christie et al. 2018). Correlated selection on life-history, physiological and behavioural traits can further maintain recurring trait combinations rather than isolated behaviours (Réale et al. 2007; Sih, Bell, Johnson, and Ziemba 2004; Wolf et al. 2007), although the favoured combinations remain context dependent (Chang et al. 2024; White et al. 2022).

Selection can also reduce behavioural diversity. Stabilising selection on behavioural phenotypes can reduce among-individual variation when intermediate behavioural expression has higher fitness than extreme behavioural phenotypes, whereas directional selection can erode variation when one behavioural phenotype is consistently favoured (Lande and Arnold 1983). Thus,

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evolutionary forces can either maintain behavioural diversity, for example through fluctuating or negative frequency-dependent selection or reduce it, for example through stabilising selection, directional selection or persistent anthropogenic selection.

Spatial sorting can also promote behavioural divergence when dispersal success differs among behavioural types (Shine et al. 2011), as suggested for fragmented rivers and barrier-associated systems including waterfalls or dams (Blondel et al. 2020) and in species such as American eels (*Anguilla rostrata*) (Mensinger et al. 2021), white-spotted char (*Salvelinus leucomaenis*) (Yamada and Wada 2023) and fat minnow (*Rhynchocypris oxycephala jouyi*) (Yamada 2024; Yamada and Wada 2023). Where such differences have additive genetic bases, they can contribute to divergence among populations and ecotypes (Cote et al. 2010; Dochtermann et al. 2019; Rittweg et al. 2024). Finally, plasticity itself can evolve, because the degree to which individuals adjust behaviour across contexts can be under genetic control and therefore exposed to selection (Dochtermann and Roff 2010; Scherer et al. 2024). Under some conditions, such plasticity may also facilitate the emergence of novel phenotypes and expose populations to new selection pressures, thereby contributing to diversification and, in some cases, speciation (Sommer-Trembo et al. 2024; Wolf and Weissing 2012; Zuk et al. 2014).

3.2 | Ontogenetic Forces

A large share of behavioural variation arises during development through phenotypic plasticity, experience and age- or stage-specific constraints (Dellinger et al. 2023, 2025; Rueger et al. 2022; Sih et al. 2015). This is especially important in fishes because aquatic communities are strongly size-structured and most fishes have indeterminate growth (Buston 2003; Persson and De Roos 2003; Urbina and Glover 2013; Versteeg et al. 2025). As body size changes, so does locomotor capacity, sensory performance, metabolic demand and vulnerability to predators, altering how individuals balance growth against safety (Ahrens et al. 2012; Werner and Hall 1979).

Behaviour therefore changes systematically over the life course. Larvae generally have lower mobility and cognitive capacity than adults (Ahti et al. 2020; Polverino et al. 2016; Wolter and Arlinghaus 2003), while maturation, hormonal changes, sex-role shifts, experience and senescence alter how fishes forage, move, compete, seek refuge and reproduce (Brown et al. 2011; Forsgren et al. 2004; Tenugu and Senthilkumaran 2022). Ontogeny thus modifies both internal state and behavioural capacity, generating behavioural differences even within the same genotype.

3.3 | Ecological Forces

Ecological conditions shape behavioural diversity at short and intermediate timescales through both predictable and fluctuating environmental variation. Light regime, temperature, oxygen availability, prey distribution, social environment (Kleinhappel et al. 2023; Snijders et al. 2021), predation risk and competition (Killen et al. 2013; Nicolaus et al. 2016; Reed et al. 2015) can all alter behavioural expression and maintain variation within populations (Kodama et al. 2012). Behavioural diversity is often high in heterogeneous or challenging habitats, where individuals may specialise on different resources or tactics and where density- and frequency-dependent interactions can promote further divergence (Bolnick et al. 2007; Braithwaite and Salvanes 2005; Janhunen et al. 2021; Webber et al. 2024).

Many of these responses are plastic. Fish adjust activity, movement and habitat use across gradients in temperature, oxygen, prey, predators and density (Nakayama et al. 2016; Prchalová, Kubečka, Čech, et al. 2009; Říha et al. 2022, 2025; Westrelin et al. 2022), and such context dependence can be described using behavioural reaction norms (Dingemanse et al. 2010). Plasticity can sometimes outweigh genetic effects (Ferguson et al. 2019; Stamps 2016), but whether the observed plasticity is always adaptive remains unresolved (Wong and Candolin 2015). Ecological forces also include socially transmitted components of behaviour, such as predator avoidance or migration routes (Aikens et al. 2024; Shumway 1999; Slotte et al. 2025), and sex-specific repertoires associated with different reproductive roles (Prchalová et al. 2022; Wearmouth and Sims 2008; Žák et al. 2020). Because behaviour can alter ecological conditions and vice versa, ecological and evolutionary forces are linked by eco-evolutionary feedbacks (Dall et al. 2004, 2012; Sih et al. 2015).

3.4 | Stochastic Forces

Stochastic events also shape behaviour, including stochastic developmental noise, random variation in neural wiring and lateralization and the amplification of small early differences through self-reinforcing feedback loops, all of which can generate stable behavioural individuality even in the absence of obvious genetic or environmental differences (Honegger and de Bivort 2018; Linneweber et al. 2020). At broader ecological scales, stochastic processes such as migratory straying (Keefer and Caudill 2014), hydrodynamically mediated variation in larval dispersal and settlement (Faillettaz et al. 2018; Lecchini et al. 2005) and storm-driven habitat disturbance on coral reefs (Gerlach et al. 2021) can move individuals or recruits into new habitats, alter connectivity among populations, and create opportunities for subsequent behavioural divergence. In salmonids, straying can introduce individuals with different migratory histories or behavioural tendencies into recipient populations, although its contribution to behavioural diversity is expected to be context dependent because straying rates and consequences differ among species, populations and life-history strategies (Keefer and Caudill 2014). Individual differences can arise in genetically identical fishes reared under uniform conditions, with small, cumulative feedback loops generating lasting divergence (Bierbach et al. 2017; Scherer et al. 2024). Random mutations and epi-mutations (e.g., DNA methylation changes, histone modifications, altered expression of non-coding RNAs), the development of novel behaviours through trial and error, and invasion by novel behavioural types all contribute to behavioural variation through stochasticity. Although stochasticity may be seen as a component of ecological forces, stochasticity is singled out here as a special case given our inability for deterministic prediction of which behaviours to expect.

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3.5 | Anthropogenic Forces

Human activities interact with all of the processes above and can alter both the amount and structure of behavioural variation by reshaping environments and fitness landscapes (Lorenzen et al. 2012; Monk et al. 2021). Because these influences are pervasive and directly relevant to management, we examine their effects in more detail in the next section.

4 | Anthropogenic Impacts on Behavioural Diversity

Behavioural responses to human-induced environmental change vary considerably within and across species (Naguib 2013; Saaristo et al. 2018). Anthropogenic pressures can influence behavioural diversity through multiple pathways, including habitat modification and exposure to novel environments and entities, which may alter selection, gene and information flow, mutation and drift (Berger-Tal et al. 2025). In fishes, these pathways involve habitat alteration and fragmentation, barriers to movement, pollution, invasions, extractive and non-extractive ecosystem utilisations (e.g., fisheries and tourism, respectively), stocking, aquaculture escapees, artificial light and noise and climate-driven shifts in ecological interactions (Arthington et al. 2016). These impacts can act directly or indirectly and may affect population persistence and evolutionary trajectories, operating from small to large spatial and temporal scales (Figure 5). Much behavioural diversity within species is expressed through within-individual variability through plasticity and predictability (Bell et al. 2009; Snell-Rood 2013). Behavioural responses may initially buffer anthropogenic change, but whether such plasticity is sufficient or consistently adaptive remains unclear, in part due to limits imposed by genetic constraints (Dingemanse et al. 2007; Wong and Candolin 2015).

FIGURE 5 | Examples of anthropogenic impacts on behavioural diversity. The middle plot depicts that these impacts tend to magnify with time and scale. Note that all impacts can be intentional or unintentional and can have direct or indirect effects.

Anthropogenic factors can directly influence activity and movement, reproductive behaviour, anti-predator responses, aggression, sociality, cognition and learning (Bertram et al. 2022; Gomez et al. 2025; Saaristo et al. 2018). Direct effects may range from the removal of behavioural phenotypes, for example through selective harvesting of bold individuals (Monk et al. 2021). Fisheries may selectively target functional groups or migration phenotypes (Árnason et al. 2009; Vähä et al. 2011), directly select behavioural traits in exploited stocks (Arlinghaus et al. 2017; Monk et al. 2021) and generate differential fishing pressure associated with stock-specific migration timing in mixed-stock contexts (Slotte et al. 2025; Wilson et al. 2025). Similarly, behavioural-trait-selective domestication in aquaculture and the release of behaviourally biased hatchery fish may alter extant behavioural patterns in the recipient community (Huntingford and Adams 2005; Lorenzen et al. 2012). Fish passage structures may also directly select for particular behaviours, potentially generating behavioural differences between populations above and below migration barriers (Haraldstad et al. 2021; Mensinger et al. 2021).

Direct interference with environmental conditions, whether through increased turbidity, introduction of chemical pollution (e.g., pharmaceuticals, industrial chemicals), or food provisioning, can also shape the diversity of behaviours present in the wild. For example, Ehlman et al. (2019) found that anti-predator behaviours of western mosquitofish (*Gambusia affinis*) became significantly repeatable under intermediate turbidity, where antipredator responses were the strongest. Guppies (*Poecilia reticulata*) exposed to environmentally realistic concentrations of an anti-anxiety pharmaceutical pollutant displayed homogenised activity levels, with among-individual variation dropping to less than half of that seen in unexposed populations (Polverino et al. 2021; Tan et al. 2020). Brown trout (*Salmo trutta*) smolts exposed to temazepam also showed decreased migration success and altered movement dynamics (Brand et al. 2024). Tourism-related feeding, for example, reduced space use in hammerhead sharks (*Sphyrna mokarran*) (Heim et al. 2024). Where neither physiological tolerance nor behavioural compensation buffers such effects, erosion of among-individual behavioural variation may affect populations and ecosystems (Bolnick et al. 2011; McCann 2000).

Behavioural diversity can also be indirectly affected by human activity, via impacts on conspecifics and interacting species or through changes in habitat structure and ecosystem processes. These indirect effects may include behavioural cascades (Fiksen et al. 2005; Romare and Hansson 2003). Human-driven removal of apex predators, for example, can alter predator–prey and competitive interactions in ways that shape ecosystem functioning (Hoover and Tylianakis 2012; Wilson et al. 2020), impacting the diversity of behaviours present. Artificial light at night can also reorganise species interactions: aquatic invertebrates aggregate in illuminated areas, which

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changes the foraging behaviour and habitat choice of fish consumers and their piscivorous predators (Becker et al. 2013). Some indirect effects operate over longer timescales by altering the evolutionary context in which behavioural diversity is maintained. Genetic pollution from escaped farmed Atlantic salmon (*Salmo salar*) is one important example from Norway (San Román et al. 2025). Because salmon home to natal rivers to spawn, local populations are exposed to river-specific selection on behavioural traits and these locally adapted traits may be eroded through interbreeding with domesticated salmon (Huntingford and Adams 2005). In addition, higher prevalence of sea lice (*Lepeophtheirus salmonis* and *Caligus clemensi*) near aquaculture facilities may alter salmon behaviour through parasitism, reduce condition and increase the risk of population collapse (Krkošek et al. 2007). Overall, anthropogenic change can modify not only how fishes behave, but also how much behavioural variation is maintained within populations and communities.

5 | Relevance of Fish Behavioural Diversity to Ecosystems and Society

Ecological and societal outcomes of behavioural diversity levels depend not only on how fishes behave on average, but also on how behavioural expression is distributed within and among individuals, groups, populations and ecotypes. The richness and evenness of behaviours present can impact individuals and their fitness, groups and ecosystems. Behavioural diversity can therefore matter when different behaviours perform differently across contexts, building resilience, when group composition alters collective outcomes, or when migratory, habitat-use, and foraging polymorphisms stabilise ecological and fishery processes. At the same time, behavioural diversity's effects are unlikely to be universally positive and remain context-, scale- and component-dependent.

5.1 | Relevance to Ecosystems

5.1.1 | Individual-Level Fitness

Behavioural diversity can matter for individual fitness because the relative fitness consequences of any one behavioural type can change depending on the composition of behaviours in the population (Campos-Candela et al. 2019; Monk et al. 2021). Boldness illustrates this clearly: bolder fishes may acquire more resources and grow faster where resources are abundant and predation risk is low (Moiron et al. 2020), but the same tendency can reduce survival in predator-rich or highly competitive environments (Hulthén et al. 2017; White et al. 2013). In largemouth bass (*Micropterus salmoides*), boldness in juveniles can enhance growth but also elevate mortality, whereas in nest-guarding adults, bolder or more aggressive individuals can achieve greater reproductive output (Ballew et al. 2017). In three-spined sticklebacks (*Gasterosteus aculeatus*), survival effects of boldness and activity depended on whether individuals were initially captured alone or in groups (Pearish et al. 2019). Such context-dependent and frequency-dependent payoffs imply that no single behavioural phenotype maximises fitness across all environments, social contexts or life stages, helping maintain multiple behavioural types within populations (Réale et al. 2007; Wolf and McNamara 2012; Wolf and Weissing 2012). More generally, recent syntheses emphasise that behavioural diversity cannot be reduced to one fixed optimum because different behavioural types can be favoured across contexts and time (Laskowski et al. 2021).

5.1.2 | Groups and Populations

Behavioural diversity is often especially important at the group and population levels, where differences in behavioural type composition can alter collective outcomes (Bibost and Brown 2013; Swaney et al. 2001). In social fishes, group composition influences collective movement, coordination, information acquisition, use and transfer, both individual and group foraging success and survival, as shown in sticklebacks (Jolles et al. 2017), guppies (Hasenjager et al. 2020), and zebrafish (*Danio rerio*) (Sbragaglia et al. 2022). Such effects arise because groups composed of different behaviours do not function identically to more homogeneous groups. At larger scales, loss of behavioural diversity can coincide with reduced population performance in some systems, but low behavioural diversity is not necessarily detrimental when stabilising selection favours an intermediate behavioural phenotype or when a narrower behavioural distribution is adaptive under stable conditions (Lande and Arnold 1983). In Atlantic cod (*Gadus morhua*), the historical contraction of diversity in spawning migrations has been associated with long-term declines in age diversity and productivity (Olsen et al. 2023). More generally, variation in migratory tactics, spawning locations, and habitat use can act as a form of bet hedging, spreading risk across time and space in unpredictable environments (Ohlberger et al. 2022). In migratory fishes, socially learned routes and collective memory may help maintain spatial behavioural diversity among contingents, with potential consequences for collapse and recovery dynamics (Chambers 2021). Conversely, behavioural patterns that are homogenous among individuals, such as schooling or habitat association, can result in hyperstable catch rates, increasing the risk that exploitation masks population decline (Dassow et al. 2020; Hočevar et al. 2021; Post et al. 2002).

Variation in movement and migratory tactics may also help populations persist under environmental change. In northern pike (*Esox lucius*), exposure to strong salinity gradients has been associated with a continuum from residency to anadromy, including intermediate partially migratory phenotypes that bridge freshwater and brackish habitats (Rittweg et al. 2024). In Atlantic cod, individual variation in personality has also been shown to explain variation in plastic responses to climate change, with reactive and proactive individuals differing in ways that may either facilitate or constrain adaptation under warming conditions (Villegas-Ríos et al. 2018). Similar dynamics may also occur during biological invasions, because individuals at invasion fronts are often a non-random subset of the source population, frequently characterised by particular dispersal-related behavioural types (Cote et al. 2010, 2013). In that sense, behavioural diversity can shape establishment and spread by filtering which behavioural phenotypes colonise novel habitats and by altering the behavioural composition of both invading and recipient assemblages (Conrad et al. 2011). Such within-metapopulation diversity may increase the number of ecological

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pathways through which persistence is possible under novel or fluctuating conditions (Ramesh et al. 2022; Sunde et al. 2022; Tibblin et al. 2016), although the strength and generality of this effect still require more direct testing.

This logic also aligns with the concept of evolutionary rescue, in which persistence under environmental change depends partly on the presence of heritable variation that allows adaptive responses before population decline becomes irreversible (Carlson et al. 2014). In fishes, this idea is relevant where behavioural and life-history diversity is coupled to genetically differentiated ecotypes. For example, Atlantic cod in coastal systems can contain distinct ecotypes that differ in movement behaviour, physiology and life history (Kristensen et al. 2021), and long-term maintenance of this diversity may contribute to persistence across heterogeneous and changing environments (Sodeland et al. 2022). However, direct evidence that behavioural diversity per se drives evolutionary rescue in fishes remains limited, so this mechanism should be treated as plausible but incompletely resolved.

5.1.3 | Trophic Interactions and Communities

Behavioural diversity can also alter trophic interactions when predators or consumers differ consistently in how, where or when they forage. Prey-side boldness altered predation outcomes in roach (*Rutilus rutilus*) depending on predator hunting mode (Blake et al. 2018), whereas predator-side behavioural differences in wild pike cichlids (*Crenicichla frenata*) predicted attack rates during prey presentations in nature (Szopa-Comley et al. 2020). Within-population diversification in hunting tactics can spread predation risk across prey species, habitats or depth strata. In great white sharks (*Carcharodon carcharias*), different individuals use contrasting hunting depths, which spatially redistributes predation risk (Papastamatiou et al. 2022). In coral reef systems, fish populations in protected areas were bolder and imposed substantially greater predation pressure on lower trophic levels than fish in fished areas, where timidity had increased through learning and possibly fisheries-induced evolution (Rhoades et al. 2019). Likewise, diel migratory behaviour often occurs in only part of a population, and the tendency to migrate can differ among behavioural types, including bold and shy individuals (Brodersen et al. 2008; Chapman et al. 2011; Žák et al. 2020). Essentially, the spread of trophic impacts can depend on both the number of behaviours present (richness), affecting foraging and their distribution (evenness) in the population.

Behavioural diversity may also map onto trophic niche, as boldness correlated with stable-isotope-based niche measures in stickleback (Theódórsson and Ólafsdóttir 2022). However, this link is not universal: personality did not predict individual niche variation in common bully (*Gobiomorphus cotidianus*) (Kerr and Ingram 2021), and some fish experiments found weak or indirect food-web effects of behavioural type composition, with biomass or growth effects dominating (Laskowski, Alirangues Nuñez, et al. 2022; Schröder et al. 2016). This suggests that behavioural diversity may matter strongly in some systems, especially where habitat structure, predation risk or spatial patchiness amplify non-consumptive effects (Madin et al. 2011; Nash et al. 2016), but less so in others (Peacor et al. 2011; Šmejkal et al. 2018).

5.1.4 | Ecosystem Function and Resilience

At the ecosystem scale, behavioural diversity may contribute to resilience when different behaviours, within and across species, buffer populations and ecosystem processes against local disturbance. In salmonids, among-population variation in migration timing and spatial structure is a well-established example of portfolio effects, whereby asynchronous behavioural, life-history or population components stabilise aggregate returns, ecosystem processes or fishery yields, and increase resilience to local stressors (Schindler et al. 2010, 2015). Straying during natal homing may contribute to such dynamics by maintaining some connectivity among population components, but its effects are context dependent because excessive gene flow or hatchery-mediated mixing can also erode local adaptation (Keefer and Caudill 2014).

Within populations, behavioural diversity can also affect ecosystem processes directly: individual-level behavioural variation in fish nutrient recycling caused nutrient-supply estimates to differ from population-average expectations in most cases, and incorporating this variation nearly doubled estimated nutrient supply, while selective harvest of more active individuals reduced nutrient supply by up to 69% (Allgeier et al. 2021). Comparable ecosystem-level effects have also been shown for stickleback and alewife (*Alosa pseudoharengus*) phenotypes that differ in their ecological impacts on prey communities, primary production and dissolved organic matter (Harmon et al. 2009; Palkovacs and Post 2009). Direct empirical tests of ecosystem resilience in the narrow sense remain rare, so links between behavioural diversity and resilience should be treated as plausible.

5.2 | Relevance to Society

5.2.1 | Ecosystem Services

Some of the strongest societal relevance of behavioural diversity comes from fisheries. For example, the salmonid portfolio effects discussed above can stabilise fishery outcomes by spreading risk across asynchronous migratory, spatial and population components (Schindler et al. 2010, 2015). In Atlantic cod, coexistence of resident coastal and more migratory offshore behavioural components historically supported different fishery sectors, and the selective loss of coastal components reduced accessibility for coastal fisheries (Árnason et al. 2009; Robichaud and Rose 2004).

Behaviour-selective fishing can also reshape the behavioural composition of exploited populations, with consequences for harvest quality and non-consumptive recreation. Angling and spearfishing often remove bolder, more exploratory, active or aggressive individuals disproportionately, although the direction of selectivity can vary by gear, species and context (Alós et al. 2016; Härkönen et al. 2016; Lucas et al. 2023; Monk and Arlinghaus 2017; Sutter et al. 2012). Over time, this can leave behind harder-to-catch and more timid populations, reducing catchability and degrading recreational experiences (Arlinghaus et al. 2017). Similar processes may affect ecotourism when fishes become more refuge-bound or less visible in heavily fished systems (Sbragaglia et al. 2018, 2024). A related

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point may apply beyond fisheries: in sharks, incident risk to humans may depend disproportionately on a small subset of bolder individuals rather than on shark density alone (Clua et al. 2024; Vignaud et al. 2023), implying that management based on random culling may overlook relevant behavioural heterogeneity (Clua et al. 2024; Clua and Linnell 2019).

Behavioural diversity can also have cultural value. For indigenous and other fishing-dependent communities, loss of diversity in the timing or intensity of spawning runs would reduce not only ecological stability but also cultural continuity and access to seasonal resources (Ryther et al. 2024).

5.2.2 | Stock Assessment, Monitoring, and Legal Issues

Behavioural diversity is highly relevant to monitoring because catchability is affected by behavioural heterogeneity. Differences in activity, feeding, habitat use, sociability, depth use and learning can all bias sampling and stock assessment. In passive gears, more active individuals or sexes may be overrepresented (Prchalová et al. 2008, 2010; Prchalová, Kubečka, Říha, et al. 2009); examples include round goby (*Neogobius melanostomus*) (Žák et al. 2018), Eurasian perch (*Perca fluviatilis*) (Heermann et al. 2013; Horppila et al. 2011; Prchalová et al. 2022), guppies (Diaz Pauli et al. 2015), sticklebacks (Kressler et al. 2021), and rainbow trout (*Oncorhynchus mykiss*) (Biro and Post 2008). In active gears and observational methods, biases can arise when sampling misses behaviourally distinct habitats, times of day, or depth-use phenotypes, as shown for bluegill (*Lepomis macrochirus*) (Wilson et al. 2011) and tiger sharks (*Galeocerdo cuvier*) (Vaudo et al. 2014). Learning also matters: naive and experienced individuals, or fishes exposed to different harvesting regimes, can differ strongly in vulnerability, which complicates mark–recapture estimates, catch-per-unit-of-effort-based inference and comparisons among protected and exploited areas (Czapla et al. 2023; Januchowski-Hartley et al. 2013; Mourier et al. 2017; Sbragaglia et al. 2018).

Because management and legal mandates often rely on such monitoring, failure to account for behavioural diversity can propagate into poor decisions. Apparent declines in catchability may be misread as declines in abundance, potentially triggering unnecessary or misdirected interventions (Arlinghaus et al. 2022). While high behavioural diversity may be desired in most cases, there is a trade-off with monitoring ability that should be recognised.

5.2.3 | Conservation and Restoration

Conservation and restoration outcomes often depend on whether released or protected fish populations retain sufficiently broad behavioural repertoires to cope with natural conditions. Behavioural diversity can be viewed as one component of population quality because populations may differ not only in abundance or genetic composition, but also in behavioural phenotypes that influence release survival, invasion dynamics, harvest vulnerability and monitoring interpretation (Álvarez-Quintero et al. 2021; Pathirana et al. 2025; Sales et al. 2023). Hatchery and captive-rearing environments can truncate or distort such repertoires, which helps explain why released domesticated fish often suffer high mortality in the wild (Lorenzen et al. 2012). By contrast, enrichment and life-skills training can sometimes improve post-release performance, as shown in salmonids (Brown et al. 2003; Hyvärinen and Rodewald 2013; Näslund 2021) and pikeperch (*Sander lucioperca*) (Holubová et al. 2026; Jůza et al. 2024), and more natural production environments can better preserve the behavioural capacities needed for foraging, predator avoidance, movement and reproduction.

Behavioural diversity needs restoration actions to preserve the ecological settings in which multiple behaviours can persist. Maintaining social structure and behavioural hierarchies may matter for conservation outcomes in social fishes (Villegas-Ríos et al. 2022). Connectivity measures, for example, do not affect all individuals equally if migratory decisions and passage performance vary among behavioural types. In Atlantic salmon, smolts with higher basal activity were more likely to use a fish passage than a turbine intake at a hydropower plant, showing that restoration outcomes can filter individuals by behavioural phenotype even when the same route is available to all fish (Haraldstad et al. 2021). This broader point is consistent with phenotype-management perspectives, which emphasise that restored systems differ in the extent to which they accommodate and retain phenotypic, including behavioural, variation (Watters et al. 2003; Watters and Meehan 2007).

5.2.4 | Fish Welfare

Behavioural diversity also matters for fish welfare in captivity because individuals differ in stress coping styles, aggression, dominance and environmental needs. Welfare problems can arise when captive systems favour only a subset of behavioural types or force incompatible types into simplified social and physical environments. In salmonid aquaculture, for example, selection for rapid growth has been associated with boldness, aggression and risk taking, potentially worsening social conditions for more risk-averse conspecifics (Castanheira et al. 2017; Huntingford and Adams 2005). Population-average welfare measures may also miss vulnerable behaviours because coping-style diversity is associated with differences in stress recovery, neurochemical profiles and responses to stocking density in cultured fishes (Alfonso et al. 2019; Carbonara et al. 2019; Höglund et al. 2020). Recognising such variation can improve housing design, enrichment, and welfare-oriented breeding or screening programmes (Boulton et al. 2018; Galhardo et al. 2008; Prentice et al. 2022).

6 | Implications for Fish and Fisheries Management and Conservation

This section considers how fish and fisheries management and conservation can incorporate behavioural diversity. We emphasise two interdependent issues: management interventions may maintain or erode behavioural diversity, and existing behavioural diversity may shape population responses to monitoring, restoration, stocking, connectivity measures, spatial protection and harvest regulations. Our objective is not to present a complete operational toolkit, nor to imply that behavioural

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diversity should be maximised as a single scalar index. Rather, we argue that natural behavioural repertoires and the ecological and evolutionary processes that generate adaptive behavioural variation should be explicitly considered in applied fish science. The following suggested actions, highlighted in bold, are motivated by previous studies that emphasise the often-overlooked, yet relevant role of animal behaviour in conservation and management (Blumstein and Fernández-Juricic 2010; Caro and Sherman 2012; Malone and Polivka 2022; White et al. 2014).

Empirical examples increasingly show that management often acts through behavioural exposure filters: behavioural variation influences which individuals encounter fishing gear, cross protected-area boundaries, locate passage structures or enter monitoring devices (Alós et al. 2016; Haraldstad et al. 2021; Villegas-Ríos et al. 2021). Thus, the management issue is not only that fish behaviour affects outcomes, but that management actions can disproportionately affect particular behaviours within behaviourally structured populations (de Benito-Abelló et al. 2022; Jones et al. 2021).

6.1 | Promote, Sustain and Maintain Behavioural Diversity

Maintaining behavioural diversity within and among populations may contribute to more stable ecological and fisheries outcomes (Ives and Carpenter 2007; Schindler et al. 2015), although the strength, direction and generality of this relationship likely depend on ecological context, the behavioural component considered, and the management objective. Among-stock variation in run timing, for example, may contribute to more stable yield provisioning (Schindler et al. 2010). Such variation can be supported through time- and area-based management, including stock-specific quotas, harvest distributed across the spawning season and spatially explicit restoration that maintains population-specific behavioural, genetic and life-history variation (Norderhaug et al. 2024; Tamario et al. 2019). From this perspective, the management aim should not be to maximise behavioural diversity as an index value per se, but to maintain or restore natural behavioural repertoires and the ecological and evolutionary processes that generate and preserve adaptive behavioural variation (Berger-Tal et al. 2025).

Fishing gears are often behaviourally selective, and repeated selective removal of particular behavioural phenotypes can erode behavioural diversity and alter population-level catchability (Arlinghaus et al. 2017; Ohayon et al. 2024). Empirical studies show that capture can select against particular behavioural phenotypes, including high activity in experimentally angled Mediterranean coastal fishes (Alós et al. 2012), boldness in common carp (*Cyprinus carpio*) (Klefoth et al. 2017), spatial behaviour and home-range use in pearly razorfish (Alós et al. 2016), and aggression or parental-care traits associated with reproductive fitness in largemouth bass (Sutter et al. 2012). However, behavioural selectivity is not universal, as boldness did not predict angling vulnerability in Eurasian perch (Vainikka et al. 2016), and repeatable encounter-related movement traits did not explain angling vulnerability in common carp or tench (*Tinca tinca*) (Monk and Arlinghaus 2017). Precautionary approaches that reduce persistent selection against particular behavioural types include temporally and spatially distributed harvest, rotated or complementary protected areas (Côté et al. 2014; Januchowski-Hartley et al. 2014), harvest slots rather than minimum-length limits where appropriate (Ahrens et al. 2020), and best-practice handling to reduce discard mortality (Brownscombe et al. 2017; Lucas et al. 2025). These measures are most defensible when framed as ways to reduce behaviourally selective mortality and preserve a broader distribution of behavioural phenotypes that may contribute to future recruitment and satisfactory recreational fishing and diving experiences, and protect ecosystem functions (Alós et al. 2019; Arlinghaus et al. 2014; Lucas et al. 2025).

Stocking and captive rearing can also reshape behavioural diversity because hatchery environments often impose selection pressures and developmental conditions that differ markedly from those in the wild (Lorenzen et al. 2012). Evidence for stocking applications is strongest for hatchery–wild or rearing-environment differences, rather than for fully quantified within-cohort behavioural diversity, so claims about restoring behavioural diversity through stocking should remain cautious (Sundström et al. 2004; Braithwaite and Salvanes 2005; Fritts et al. 2007). Hatchery selection promoted boldness in brown trout fry, and boldness was linked to dominance, indicating that captive propagation can shift the behavioural phenotype distribution released into the wild (Sundström et al. 2004). Variable early rearing generated more behaviourally flexible Atlantic cod (Braithwaite and Salvanes 2005), whereas hatchery-origin spring Chinook salmon (*Oncorhynchus tshawytscha*) fry were more vulnerable to predation after one generation of hatchery culture, suggesting that release quality should include behavioural competence as well as size, number, and genetic origin (Fritts et al. 2007). Rearing environments that include greater spatial complexity, lower densities where feasible (Brockmark et al. 2010), varied flow conditions, diverse feeding regimes (Conrad et al. 2011), and life-skills training (Braithwaite and Salvanes 2005) may therefore help maintain or induce behaviourally relevant repertoires, but their effects on post-release performance and on the distribution of behavioural phenotypes in released cohorts should be evaluated explicitly (Hyvärinen and Rodewald 2013; Näslund 2021; Näslund and Johnsson 2016).

For conservation stocking, maintaining phenotypic and genetic variation in broodstock and reducing artificial selection during breeding and rearing are therefore important for avoiding the release of behaviourally narrowed cohorts (Harada et al. 1998; Shumway 1999; Watters and Meehan 2007). Where feasible, restoration that facilitates natural recruitment and continued exposure to wild ecological and selective conditions is likely to maintain behavioural diversity more effectively than repeated stocking interventions (Hühn et al. 2014; Radinger et al. 2023).

6.2 | Behavioural Diversity-Informed Approaches in Monitoring, Welfare, and Conservation

All sampling gears used to index wild fish abundance are behaviourally selective (Arlinghaus et al. 2017; Diaz Pauli and Sih 2017; Kubečka et al. 2012). Loss of certain behavioural phenotypes through fisheries over time that reduce population-level catchability will reduce the value of samples taken by common

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fishing gears, for example, catch-per-unit effort data taken by rod-and-line or nets (Alós et al. 2019; Prchalová et al. 2008; Prchalová, Kubečka, Říha, et al. 2009). As such, new methods of monitoring must be identified to properly monitor population trends. One option is to use multiple complementary gear types (Kubečka et al. 2012; Říha et al. 2023) and incorporate less extractive methods such as video-based approaches (Alós et al. 2015; Holubová et al. 2025), so as to minimise the potential for gear biases affecting inferences drawn from monitoring efforts.

Aquaculture and captive conservation programmes should account for behavioural diversity because individuals can differ in stress responsiveness, aggression, dominance, risk-taking, and environmental requirements (Browning 2023; Huntingford and Adams 2005). Systems that favour only a narrow subset of behavioural phenotypes may improve performance for some individuals while reducing welfare or post-release suitability for others (Castanheira et al. 2017; Macaulay et al. 2021). Behavioural screening so that the more stress-resilient individuals are cultured for human consumption, environmental enrichment, and breeding objectives should therefore be evaluated not only against mean performance but also against their effects on the distribution of behavioural phenotypes retained in captive or released cohorts (Boulton et al. 2018; Prentice et al. 2022).

Connectivity measures can also filter behavioural diversity when passage success differs among behavioural phenotypes. Fish passage facilities are central mitigation tools for restoring longitudinal connectivity (Silva et al. 2018), but inappropriate designs may favour only some behavioural types and thereby contribute to fragmented subpopulations and loss of behavioural diversity (Haraldstad et al. 2021). For example, small experimental barriers favoured larger, bolder, and faster-swimming river-resident individuals, with repeatable passage behaviour documented in brown trout (Jones et al. 2021). In American eel, personality and body length influenced experimental fishway passage (Mensinger et al. 2021), whereas behavioural type did not predict nature-like fishway passage in rainbow smelt (*Osmerus mordax*), suggesting that environmental or morphological factors can override behavioural type in some systems (Landsman et al. 2017). Where barriers cannot be removed, fish passage design and evaluation should account for variation among individuals (Smederevac-Lalić et al. 2025), life stages (Beeman et al. 2012), body sizes, migration timing, habitat preferences and movement tendencies (Prchalová et al. 2011; Prchalová, Slavík, and Bartoš 2006; Prchalová, Vetešník, and Slavík 2006).

Individual-level telemetry, imaging, sonar and biologging data can help quantify management-relevant components of behavioural diversity when analyses retain among-individual and within-individual variation rather than collapsing behaviour to population means (Beumer et al. 2026; Conrad et al. 2011). Standardised movement traits, such as displacement, range size, area-use intensity, diel activity and individual reaction norms, may be particularly useful for assessing movement-related components of behavioural diversity in monitoring and restoration contexts (Beumer et al. 2026). Applied tools reviewed by Malone and Polivka (2022), including isodars for habitat selection and restoration assessment and giving-up densities for patch use and perceived predation risk, may also help quantify selected components of behavioural diversity when individual- or population-level variation is explicitly measured.

Restoring natural processes and habitat heterogeneity is likely to be important for maintaining behavioural diversity in human-modified waterscapes (Watters et al. 2003; Watz et al. 2020). In highly modified systems where full process restoration is not feasible, mitigation can still aim to preserve conditions that allow multiple behavioural phenotypes to persist, such as improved connectivity, flow heterogeneity, refuge availability and habitat complexity (Lott 1991; Watters et al. 2003; Watz et al. 2020). Such measures should be framed cautiously as approaches expected to maintain ecological settings in which behavioural diversity can be expressed, rather than as universally demonstrated tools for increasing behavioural diversity across systems (Watters et al. 2003; Watz et al. 2020).

6.3 | Sustainable Fisheries

Area-based management can interact strongly with behavioural diversity because individuals differ in home-range size, habitat use, movement and vulnerability to harvest (Minns 1995; Villegas-Ríos et al. 2017). Protected areas that encompass only part of the space-use distribution may protect some behavioural phenotypes more effectively than others and thereby generate behaviourally selective harvest outside reserve boundaries (Januchowski-Hartley et al. 2014; Ohayon et al. 2024). No-take areas and marine protected areas can protect movement phenotypes unequally. In white seabream (*Diplodus sargus*), individuals clustered into residents, commuters, seasonal visitors and single users, and these spatial behavioural types differed strongly in time spent at risk outside a no-take area (de Benito-Abelló et al. 2022). In anadromous brown trout, or sea trout, home-range size was repeatable and selection on this movement trait differed between a no-take reserve and fished areas, suggesting that reserve networks spanning habitat heterogeneity and fishing-pressure gradients may better preserve movement diversity than isolated protected areas (Thorbjørnsen et al. 2021). Similarly, in a Norwegian marine protected area, Atlantic cod, pollack (*Pollachius pollachius*) and ballan wrasse (*Labrus bergylta*) individuals with larger and more dispersed home ranges, especially near reserve borders, spent more time exposed to fisheries and were more likely to be harvested, showing how among-individual movement variation can shape both protection and harvest selection (Villegas-Ríos et al. 2021). More broadly, protected areas smaller than the routine space use of target fishes are less likely to deliver strong local density benefits, indicating that movement phenotypes should inform reserve size and network spacing where such data are available (Di Franco et al. 2018). Behavioural diversity-informed spatial management should therefore consider the distribution of home ranges and movement strategies within target populations, while also maintaining evidence-based controls on fishing mortality outside protected areas.

The objectives of spatial protection should be stated clearly because reserve design may differ depending on whether the primary aim is biodiversity protection, maintenance of behavioural diversity, fisheries enhancement through spillover or a combination of these goals. When spillover is an explicit objective, protection may intentionally cover only part of the movement

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distribution. This should be balanced against the risk that more mobile or less risk-averse behavioural types experience higher fishing mortality outside reserve boundaries (Januchowski-Hartley et al. 2014; Ohayon et al. 2024).

Artificial aggregation (Davies et al. 2014) or refuge structures (de Moraes et al. 2023; Nagayama and Nakamura 2010; Salmon et al. 2025) may alter behavioural diversity if they concentrate fish with particular space-use, dominance, refuge-seeking or risk-taking phenotypes, especially when fishing pressure is high around those structures. Because direct evidence for effects on behavioural diversity remains limited, these structures should be monitored for disproportionate attraction or exposure of particular behavioural types, rather than assumed to benefit all phenotypes equally. Maintaining sustainable fishing mortality around such structures is therefore important to avoid amplifying behaviourally selective harvest (Ohayon et al. 2024).

Overall, sustainable fisheries management should treat behavioural diversity as a component of intraspecific diversity that may affect catchability, monitoring accuracy, protected-area performance, stocking outcomes and resilience to environmental change. The available evidence supports a precautionary focus on reducing persistent behavioural selectivity, maintaining habitat and process heterogeneity, and monitoring among- and within-individual behavioural variation where data allow; however, empirical demonstrations of management programmes explicitly designed around behavioural diversity remain scarce.

7 | Future Outlook

At present, several major knowledge gaps continue to constrain the systematic incorporation of behavioural diversity into conservation and management. First, behavioural diversity remains difficult to quantify in ways that are both comparable and scalable across species, populations, and ecosystems. This highlights the need for robust and standardised metrics, indicators, and analytical frameworks capable of linking individual-level behavioural variation to population- and community-level processes. Movement-related traits derived from telemetry, biologging, sonar and video data provide one promising route, particularly when they retain repeated individual-level observations, environmental context, and among- and within-individual variation. However, such traits represent only one measurable component of behavioural diversity and should not be treated as a proxy for behavioural diversity as a whole. Second, empirical support remains limited, particularly from long-term, comparative and manipulative studies able to test how behavioural diversity influences ecosystem stability, food-web dynamics, resilience, productivity and catchability under ongoing environmental change. Third, it remains unresolved which hierarchical components of behavioural variation—among-individual differences, within-individual plasticity, predictability or among-population variation—are most consequential for ecological and management outcomes, and whether their effects are generally positive, neutral, negative, or non-linear. Fourth, behavioural data remain insufficiently integrated with genetic, trophic, demographic, and environmental information, thereby constraining inference about the mechanisms that generate, maintain or erode behavioural variation. Finally, applied examples remain scarce, and there are still few case studies demonstrating how the explicit consideration of behavioural diversity can meaningfully alter management, restoration, or conservation decisions in practice. Addressing these gaps will be essential if behavioural diversity is to be incorporated into predictive models, fisheries management and broader biodiversity-conservation strategies.

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Conflicts of Interest

Robert Arlinghaus is an Editor of Fish and Fisheries, but was not involved in the handling and decision-making of this manuscript.

Data Availability Statement

The authors have nothing to report.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Emerging technologies that allow studying fish behavioural diversity. Technological advancements are revolutionising ecological studies, introducing novel tools such as camera traps combined with detection and classification algorithms that efficiently monitor wildlife. However, the application of such technologies in behavioural studies introduces significant challenges. Capturing relevant behavioural components demands not only highly detailed data (e.g., animal pose estimation for interactions with the environment and other individuals), but also data collected over extended temporal scales to adequately reflect the intricacies of animal behaviour. Another critical issue is the impact of technology on natural behaviours. The technologies employed must be non-intrusive to ensure that the data collected reflect genuine behaviours that are undistorted by the presence or influence of the monitoring equipment.

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