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The behavioural ecology toolkit for fish management and conservation

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Abstract

Fishes include some of the most threatened vertebrate species globally. As such, efforts to effectively conserve and manage fish populations and their habitats are vast. Here, we present conceptual tools from behavioural ecology to establish a framework for studies of fish conservation and management, connecting questions relevant to managers and practitioners with behavioural theories and methodologies. We apply predictions developed from a theory to diet choice, patch use, habitat selection, movement, and social behaviours. We present questions and issues in fisheries management and conservation for which theory, hypotheses, and methodologies would be both novel and complementary to current assessment strategies or conservation efficacy studies. In each case, theory approaches the ecological trade-offs associated with a given behavioural trait through the lens of adaptations and fitness implications—the foundational principles of behavioural ecology. We show key methodologies used to effectively apply behavioural theory to specific hypotheses relevant to a given management question. We then compile the conceptual and methodological approaches to assemble a toolkit through which fisheries managers may assess, for example, habitat selection behaviours via novel study designs and/or new ways of interpreting commonly collected data (e.g., distribution and abundance relative to habitat type). Finally, we propose training of aquatic and marine natural resource specialists and conservation agency fish biologists be complemented with behavioural ecology theories and methodologies.

KEYWORDS
diet choice, fisheries management, habitat selection, movement, patch use, social behaviour

1 | INTRODUCTION

On a global scale, fishes include some of the most threatened vertebrate species, owing to climate change, invasive species, habitat degradation, overfishing, and other anthropogenic threats (Burgess et al., 2013; Cowx, 2002; Heino et al., 2009; Su et al., 2021). Conservation and restoration ecology across taxa and ecosystems evaluate the response of species or populations to these environmental perturbations. Given the ecological benefits fishes have for the maintenance of healthy ecosystems (Cinner et al., 2020), and the economic benefits of healthy fish populations as food sources (FAO, 2020), for recreational and commercial fishing, and ecotourism (Cinner, 2014; Lynch et al., 2016; Sala et al., 2018), efforts to effectively conserve and manage fish populations and/or restore their habitats are vast (Cooke et al., 2005; Roni et al., 2008; Williams et al., 2016; Upper Columbia Regional

Technical Team, 2017). Perturbations, and efforts to ameliorate them, have measurable ecological responses that can evaluate the efficacy of restoration and conservation. These responses include behavioural traits (e.g., foraging, habitat-related movements, and social interactions) that, unlike basic observations of distribution and abundance, can be described by a complex body of theory that adds important mechanistic details to such evaluations. Indeed, behaviour reflects the influence of the environment on individual fitness (Berger-Tal & Saltz, 2016) and therefore is relevant to environmental management, including that directed at fishes.

This body of theory comprises behavioural ecology—the study of behaviours as adaptive traits that maximize fitness within a given ecological context. Behavioural ecology thus demonstrates how behaviour can indicate environmental quality and the effectiveness of conservation/management programs (Berger-Tal & Saltz, 2016). Such application to fisheries biology could contextualize the effectiveness of conservation efforts in terms of fitness consequences. This is because successful conservation and recovery will affect the survival and reproductive rate (both components of Darwinian fitness) of individuals in the target species. Theoretical and practical applications from behavioural ecology mechanistically link observable behavioural traits to fitness (Conrad et al., 2011; Sih et al., 2004). Direct measurement of fitness in fishes is difficult because it is typically intractable to quantify the number of surviving, reproductive offspring (the most direct measure of fitness) in species that have complex mating systems, broadcast spawning, or migrate to separate reproductive habitats. Nevertheless, many of the tools from behavioural ecology that we will describe below are focused on response variables that are good correlates of, or proxies for fitness, such as foraging costs of predation, density dependence, and energetic intake, and how they may be good metrics of conservation effectiveness.

Individual differences in fitness result from behavioural phenotypes that vary across the environment in a consistent way. Like other traits, these phenotypes are continuous and may be optimal solutions to variable selection pressures in the environment (Mittelbach et al., 2014). Behavioural ecology can therefore assess the potential for behaviours to optimize fitness depending on how fitness is shaped by the ecological context (Mittelbach et al., 2014; Sih et al., 2012). Thus, behavioural ecology can provide managers with the ability to evaluate the response of fish to environmental perturbations and to efforts to ameliorate them. Because behavioural ecology informs the conservation and management of threatened species (Morris et al., 2009), including fishes (Brooker et al., 2016; Dill, 2017; Shumway, 1999), we propose that conservation can benefit from an explicit framework for the application of behavioural ecology theory to myriad conservation questions, complementing descriptive studies of behaviour.

Extensive literature from the past decade documents the field of conservation behaviour (Berger-Tal & Saltz, 2016; Blumstein & Fernandez-Juricic, 2010; Conrad et al., 2011). There is also a growing body of literature investigating behavioural responses of fishes to conservation and management efforts (Bergseth et al., 2016; Januchowski-Hartley et al., 2015; Samia et al., 2019). Conservation questions of interest to fisheries managers may include marine reserve design, predator management, the effects of introduced species (competition, predation, etc.), habitat restoration effectiveness, and projections of population growth (related to diet, foraging efficiency, and patch use). These questions often lead managers to seek whole-population-level, large-scale solutions, whereas behavioural responses are commonly viewed as functioning at the individual level and therefore too variable for broad application. However, behavioural ecology addresses the contextual basis of responses to environmental variation, which can avoid confounding our efforts to use behaviours to evaluate the broad application of management strategies. Because behavioural ecology views behaviours through the lens of adaptations and ecological trade-offs, practitioners can effectively apply behavioural theory to test hypotheses and evaluate the efficacy of techniques or approaches used to conserve fishes.

Below we emphasize how behavioural ecology can be used to develop focused studies for strategic fish conservation and management. For example, diet choice analysis involves the description of the relative proportion of food resources consumed, but optimality theory evaluates the selected proportions in terms of the net energy gained via a given strategy and the predicted fitness of each strategy. Habitat protection, enhancement, or restoration are common conservation strategies. Behavioural ecology offers several approaches via habitat selection theory that can be used in an evaluation of the fitness implications of habitat

selection rather than the reporting of simple correlations between habitat and abundance. In some cases, fisheries managers may not be required to collect extra data, but can approach existing data (biomass, abundance, and size-class) in new ways to attain a robust understanding of the ecological processes that affect the success of conservation efforts (Dall et al., 2004; Stamps & Swaisgood, 2007).

We present the behavioural ecologist's toolkit for the conservation of fishes. We describe diet choice, patch use, habitat selection, movement, and social behaviours, and how ecological processes may modulate these behaviours. Within each, we describe ecological trade-offs (such as those associated with habitats of varying quality) and how the diversity of behaviours present can be evaluated in terms of fitness-correlated responses to conservation actions using theoretical tools. We then describe the predictions from theory and how they warrant consideration in a conservation context for fishes and their habitats with a discussion of which methods and approaches might be most appropriate for a given context. Often these theoretical tools come from "classical" literature because the conceptual framework has been widely available for a long time with little application to fish conservation. We try to link this older literature with relatively contemporary studies to set a modern context in which the toolkit may be applied. We therefore distinguish our review from other recent reviews of fish behaviour studies that are more descriptive (Brooker et al., 2016; Samia et al., 2019) by our focus on the specific theoretical tools. Finally, we synthesize the conceptual approaches to develop a prospectus for the toolkit to assess conservation actions, their consequences, and their potential limitations.

2 | THE BEHAVIOURAL ECOLOGY TOOLKIT

2.1 | Diet choice

The choices fishes make of what to eat inform conservation and management by answering fundamental questions about the relative importance of food sources. Thus, the key management question is usually, how available are the most important food types? Studies that quantify diet breadth and overlap among species can identify the effects of food competition, including between native and invasive species with similar diets, or direct predation. Behaviours under selection may include individuals that successfully shift their diets in response to changes in the availability of the preferred food, those that consume widely from available resources (generalists), and dietary specialists. Such behaviours may be constrained when specific morphological traits, for example, are associated with a given feeding strategy. Optimal diet choice theory is a framework for evaluating these strategies in terms of fitness implications and can be a useful tool for managers to assess whether management strategies involving the status of food resources are resulting in optimal or suboptimal behaviour.

The study of diet choice behaviour for the conservation and management of fishes often uses descriptive approaches such as measurement of consumption via direct observations or gut content analyses, including metagenomics. Stable isotope analysis identifies the source of carbon or nitrogen, relative trophic positioning (Hesslein et al., 1991; Vander Zanden et al., 2015), and can indicate behavioural or ontogenetic patterns in the use of major habitat types (Heady & Moore, 2013; Litz et al., 2017; McIntyre et al., 2006). Indices (i.e., Shannon diversity index, index or relative importance, etc.) may be used to describe the diversity of fish diets (Hyslop, 1980; Pinkas, 1971; Saikia, 2012), identify overlap among competitors (Krebs, 1989; Medeiros & Arthington, 2014) and are still commonly used, including in species of commercial interest (Heng et al., 2018; Kalogirou et al., 2012). Emerging technologies, such as dietary metabarcoding—the amplification of DNA/RNA of multiple taxa in stomach contents—provide exciting new ways to assess fish diets and resolve fine-scale trophic interactions (Casey et al., 2019). Although descriptive studies may inform conservation efforts such as supplementation, they may lack the ability to make predictions about the effects of shifting food availability on the responses in a population, species, or among species.

From behavioural ecology, optimal diet choice theory enables the prediction of foraging strategies that maximize energy gain per handling time (e/h), given the variation in the availability of food or prey type (Gaeta et al., 2018; Pulliam, 1974; Stephens & Krebs, 1986). Preferences of individuals change according to resource availability usually leading to selective or opportunistic foraging behaviours. In a productive environment, or when in good body condition, foragers can afford to be selective upon nutritionally rich and readily available prey/resources, particularly if they are better competitors to begin with. In a depleted environment, when in poor body condition, or given lower competitive ability, individuals should be opportunistic and diets will likely consist of nutrient-poor resources (Hempson et al., 2017; Svanbäck & Bolnick, 2005, 2007). Switching between these behaviors is predicted to occur when the relative abundances of higher and lower nutrient prey change over time (Kotler et al., 2016).

Optimal diet theory is a tool that expands upon descriptive diet studies by allowing managers to assess selective and opportunistic consumption relative to management actions. These assessments can evaluate the potential effectiveness of management strategies such as food supplementation or whether the mitigation of competition affects the diet breadth of focal species (Heng et al., 2018; Svanbäck & Bolnick, 2005, 2007). For example, when dietary overlap shows that non-native freshwater fishes compete with native communities, native species may shift to lower-quality food (Declerck et al., 2002) or have some resilience to the effects of non-natives by virtue of high omnivory (i.e., diet breadth; Pilger et al., 2010), consistent with the predictions of the theory. If omnivores shift to lower-quality food this would indicate a need to prioritize mitigating competitive effects through control of non-native populations. Likewise, managers may assess a focal species' ability to modulate diet choice behavior in response to

environmental changes in resource availability. These responses, or lack thereof, may be informative to managers. For example, native coral reef fishes may be faced with the loss of their primary food, coral, due to bleaching events. Some species face local extinctions due to behavioural inflexibility (Brooker et al., 2014), whereas others may respond by increasing diet breadth (Feary et al., 2018), or by changing the relative proportions of food consumed. Specialist species of concern with a lack of behavioural flexibility may require supplementation or ex situ conservation interventions if food limitation is the primary issue.

These examples demonstrate the utility of using quantitative methods (diet breadth/overlap indices) in combination with theory to describe the consequences of varying behavioural responses to environmental perturbations. This approach enables practitioners to describe how conservation-related manipulations of energy flow through food webs might have consequences for populations and communities. Thus, diets of focal species compared to food availability can inform managers of the bioenergetic and physiological correlates of populations. Finally, metabarcoding may reveal unique functional roles fishes play (such as dietary specialists) and be used as a tool to indicate species for conservation. While evaluating diet choice behaviour, managers should consider potential constraints that may hinder an organism from foraging optimally, which may include lack of plasticity, morphological constraints, or lack of information on resource availability.

2.2 | Patch use

Patch use behaviours are the choices fishes make of how to occupy and use resource patches within a heterogeneous environment where resources are unevenly distributed in space and time. This body of theory is not commonly used in conservation ecology (Kotler et al., 2016), but has the potential to be combined with habitat selection data (see Section 2.3) to inform managers about habitat quality. Behaviours include the time spent in a patch, the extent to which resources are exploited in that patch and which of those resources individuals select such that patch use is optimized. These behaviours can, in turn, be studied to address conservation and management questions such as: how do variation in predation risk and resource availability impact the behaviour of fishes? How do these behaviours indicate how individuals and populations are responding to habitat modification or restoration? What are the implications of these behaviours for population dynamics? Has a focal population reached its carrying capacity? Is an ecological phase shift (i.e., the major change in the structure and functioning of the ecosystem) occurring as a result of environmental change, degradation, or conservation-oriented manipulations? How does predation risk, specifically its non-lethal effects on behaviour, impact the study population? The patch scale may therefore be one of the most informative scales at which to study fish-habitat relationships. However, because patch size varies among species and even individuals, understanding the appropriate scale at which to measure patch use may be necessary before the application of the theory to conservation questions.

2.2.1 | The "giving-up density"

We can use classical patch use theory to make testable predictions about how organisms will maximize their return for time/effort invested while foraging (MacArthur & Pianka, 1966). According to the marginal value theorem, a forager will deplete a food patch until the costs associated with foraging outweigh the rewards, at which point the forager will move to another patch where the cost is less (Charnov, 1976). An organism behaving optimally should quit foraging at this point, known as its quitting harvest rate (QHR; Figure 1a). Brown (1988) expanded upon this early theory and developed an experimental approach, the giving-up density (GUD), which estimates the QHR of a forager in terms of the quantity of food left at the patch when the forager stops foraging. The GUD incorporates metabolic costs (C), predation risk (P), and missed opportunity costs (MOC): GUD = C + P + MOC. In the experimental quantification of GUDs, C and MOC can ideally be held constant; thus, GUDs quantify, in energetic currency (food biomass), the cost of predation across patches in the landscape, which is then assumed as (negatively) correlated with fitness (Brown & Kotler, 2004).

The GUD can be quantified in the field using two experimental approaches, assuming the C and MOC components are equal at the treatment scale. The first approach is to use a "natural" resource patch. Such a resource patch must have not only a known quantity of food but also diminishing returns: as an organism forages from the patch, it becomes more difficult or costly to remove subsequent food items. The starting and ending quantities of that resource must be measured as well and it may be necessary to use averages across several patches for both metrics (Alofs & Polivka, 2004; Polivka, 2007). Manipulations of natural resource patches can be difficult because not all resource patches are equal: some are rich, and others are poor. This can have implications for how thoroughly a forager depletes a patch. The second approach quantifies the GUD with experimental food patches in field experiments. In this case, a known and consistently replicated quantity of food is embedded within the substrate (Figure 1b) and the food patches exhibit diminishing returns as previously described. A final requirement is controlling for one or more of the other costs associated with foraging at a patch. This is managed by either directly manipulating or quantifying background resource availability, predation risk, or an individual's state (Kotler et al., 2010). Behaviours range along a continuum from bold risk-takers (Alofs & Polivka, 2004) to more risk-averse species that forage less (Luttbeg & Sih, 2010; Sih et al., 2004, 2012). GUDs can serve as a proxy for fitness by measuring energetic intake and ultimately the costs of behaviours associated with a given level of risk-taking.

There are several examples showing how researchers have successfully applied GUDs to quantify the patch use of marine and freshwater fishes (Alofs & Polivka, 2004; Hedges & Abrahams, 2015;

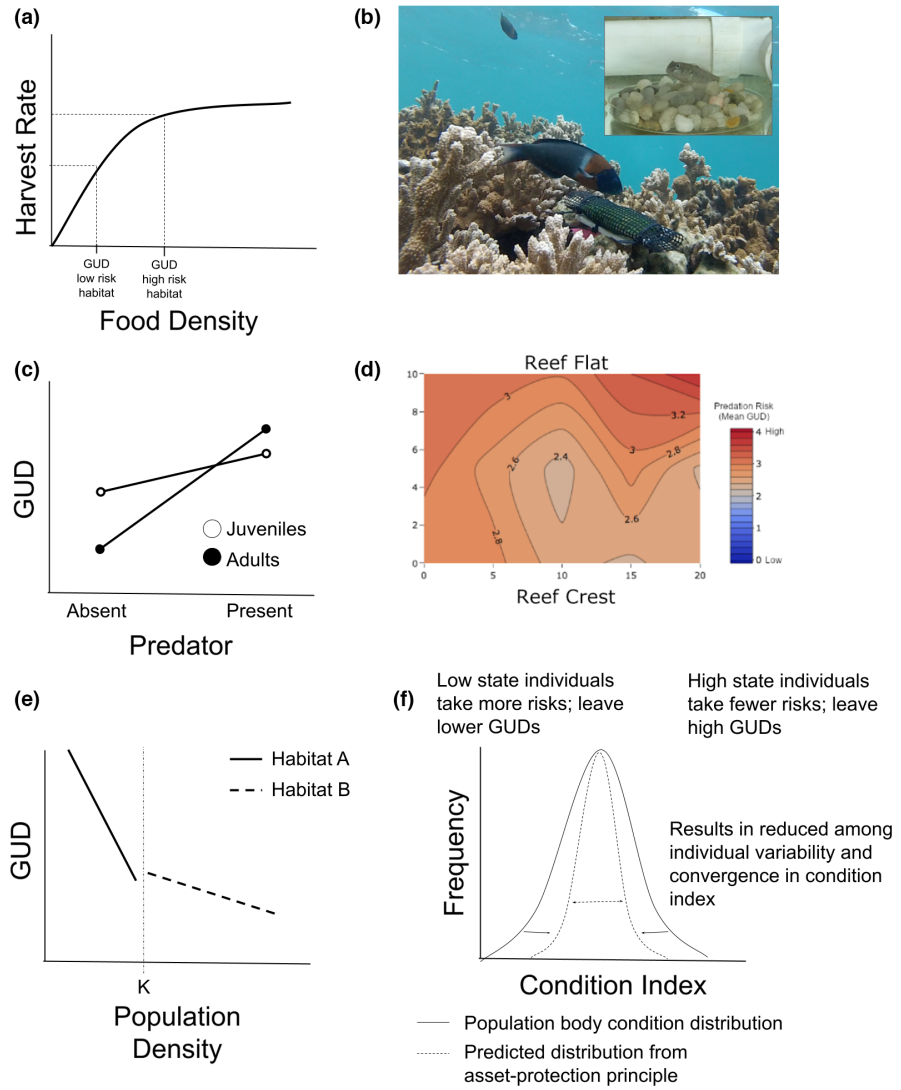

FIGURE 1 The application of patch use behaviour to the conservation and management of fishes. (a) The quitting harvest rate, measured by the GUD, at a resource patch diminishes over time. A forager at a patch with a high risk of predation has a higher GUD than a forager at a low-risk patch (Brown & Kotler, 2004). (b) Example experimental food patches which represent high-quality transient food sources for a coral reef fish in situ and a round goby (*Neogobius melanostomus*, Gobiidae) in experimental aquaria (insert). (c) Giving-up densities (GUDs) of adult and juvenile sculpins (Cottidae) are higher in the presence of a predator within experimental enclosures (after Polivka, 2007). (d) GUDs across a coral reef habitat reveal the landscape of fear for a coral reef fish, where warm colors indicate high GUD/risk, and cool colors low GUD/risk (GUD = number of krill/patch) (Malone et al., 2021). (e) GUDs at varying population densities reveal carrying capacity with an abrupt shift in slope once a population reaches its carrying capacity (Morris & Mukherjee, 2007). (f) Asset protection principle (Clark, 1994) predicts convergence in condition among individuals in a population as risk-taking behaviours are condition-dependent. Individuals in good condition take few risks and make gains slowly, whereas individuals in poor condition must take more foraging risks and gain in a condition more rapidly. Fitness may be optimized or maximized at this point because further attempts to increase condition through foraging would involve additional exposure to predation risk (Clark & Ekman, 1995; Nonacs, 2001; Figure after Polivka, 2011).

Malone et al., 2021; Petty & Grossman, 2010; Polivka, 2007). Those studies show that GUDs are effective tools, particularly for species that forage on patchy resources such as herbivorous fishes or those with demersal or benthic prey. Species such as sculpins (Cottidae) may respond well to experimental manipulations in enclosures where resource availability and predation risk can both be allowed to vary (Figure 1c; Polivka, 2007). Over larger spatial and temporal scales the GUD can reveal seasonal variation in missed opportunity costs due to changes in background resource availability (Hagy et al., 2017; Whelan & Jedlicka, 2007). The GUD approach can also be used to predict a fish's "landscape of fear" (Gaynor et al., 2019; Laundré et al., 2001; Malone et al., 2021) and how predation and anti-predator vigilance vary with habitat type a the landscape scale. The saddle wrasse (*Thalassoma duperrey*, Labridae) inhabits coral reefs in Hawaii with patchily distributed resources and varying degrees of habitat degradation that are under management. GUDs showed that saddle wrasse perceived greater predation risk on degraded reefs compared with those that were not degraded, thus

demonstrating the landscape of fear concept (Malone et al., 2021; Figure 1d), which follows from the assumption that background resource availability is variable and that GUDs will track availability relative to risk (Alofs & Polivka, 2004; Polivka, 2007). The benefit of the GUD is that it quantifies risk within a system from a forager's perspective in a biologically meaningful way—leaving more items of food in riskier patches.

When managers are concerned about predators, studies of the distribution and consumption rate of a focal species by its predator(s) may not reveal the fitness consequences indicated by shifts in behaviour (e.g., increased vigilance and reduced consumption) in response to predators. GUDs can reveal these effects and may be worth measuring, despite there being more costly in terms of time and effort. Such consequences may result in observable declines in body condition due to reduced or altered foraging behaviours, where poorer condition mesopredators indicate higher predator abundance (Barley et al., 2017). As a special case of predation, GUDs could potentially be used to evaluate foraging or habitat shifts (Section 2.3) by fishes in the face of human activity (where harvest or recreation is substituted for predation). For example, high human activity may elicit anti-predator responses in some species of fishes (Frid & Dill, 2002). If so, GUDs in such areas would be higher. We must also consider that human activity favours bold species, or species that benefit from feeding or food supplementation, which may result in lower GUDs for those species. Similar behavioural responses were observed with reduced flight initiation distance (FID) in areas with a high level of human activity (Cole, 1994; see also Section 2.4). Additionally, the fishing intensity may differ between the interior and exterior of marine protected areas, likely resulting in different patch use behaviours among individuals in a population. We expect higher GUDs if fish respond similarly to recreational fishing as they do to predation risk. Bergseth et al. (2016) found differences in perceived risk (as measured by FID) across no-entry areas and no-take areas. Finally, manipulations of food availability or measurement of patch scale variability may be intractable if the primary food source of the species of interest does not vary across the boundary of conservation areas.

At the population level, GUDs can provide valuable insights (Kotler et al., 2016). When a population has reached its carrying capacity, *K*, individuals are expected to show a decrease in foraging (with a lower GUD at *K*) at an experimental food patch (Figure 1e). Thus, managers can identify carrying capacity via a distinct shift in GUDs from higher to lower as population size increases (as observed in terrestrial systems; Morris & Mukherjee, 2007). More broadly, GUDs can be implemented into monitoring programs to predict declining or increasing population trajectories (as hypothesized in Whelan & Jedlicka, 2007). In this application, GUDs vary according to known risk factors and measure environmental quality. Population responses to changes in habitat quality and foraging area have been assessed in marine and aquatic systems (e.g., Davis et al., 2017; Nash et al., 2012; Tootell & Steele, 2016), but have not been formally tested with GUDs. Therefore, we suggest that more work should be done to empirically test these predictions in aquatic and marine systems to link GUDs to population trajectory and habitat quality. Such tests may guide appropriate conservation actions (e.g., which habitats, if conserved, might lead to population increase).

The GUD can also reveal aspects of a community or ecosystem (Berger-Tal & Saltz, 2016). For example, GUDs of benthic fishes serve as an indicator of ecological phase shifts that can lead to ecosystem collapse in shallow lakes (Persson & Nilsson, 2007). When lakes are in a clear, macroalgal dominant state they are resilient to shifts to a turbid, phytoplankton dominant state. In the macroalgal dominant state, fish showed (1) high GUDs, indicating high missed opportunity costs due to high background prey availability and (2) patch use patterns that indicated a high relative risk of predation (Persson & Stenberg, 2006). GUDs of benthic fishes shifted prior to the phase shift, thus indicating that missed opportunities decreased and relative predation risk was low. Therefore, managers can track GUDs to identify when abatement strategies, such as stocking piscivores or removing benthivorous fishes, need to be initiated to prevent ecosystem collapse (Persson & Nilsson, 2007).

GUDs could also be integrated with social foraging theory (Giraldeau & Caraco, 2018) which has been applied to shoaling and schooling fishes (Ioannou et al., 2011; Pitcher & House, 1987; Ward et al., 2012). Information on the distribution of food can be transmitted to individuals in a group and the relative success of conspecific cues may depend on group size and individual proximity to the group (Webster & Laland, 2012). This has implications for how quickly a food patch may be located, how much time is spent foraging at a given patch, and patch use by focal individuals can be evaluated in terms of the quality of social cues (Ioannou et al., 2011; Pitcher & House, 1987). Patches may be depleted more thoroughly owing to the tendency of individuals foraging more efficiently as group size increases (Day et al., 2001), though foraging opportunities can vary from individual to individual in the group (Hirsch, 2007). Importantly, group size is also important for anti-predator vigilance (Ioannou, 2017) where predation selects for larger groups (Grand & Dill, 1999; Herbert-Read et al., 2017), which leads to foraging increases that are quantifiable using GUDs (Stenberg & Persson, 2005). We further discuss social behaviours in Section 2.5.

Based on the above examples, GUDs have strong potential for use by conservation biologists and resource managers worldwide, despite a limited previous application to aquatic organisms and habitats. This slow development is likely because the techniques are sometimes difficult to apply (Bedoya-Pérez et al., 2013), particularly in aquatic systems. Performing GUD experiments may be more time-consuming than collecting total population density data, but sometimes GUDs can be estimated from forager distributions relative to their food (Polivka et al., 2013). Additionally, there are still gaps in knowledge of diet and preferred food for many species which may make it difficult to use this approach, as well as the constraints on optimal foraging presented in Section 2.1. Furthermore, most fishes are carnivorous or omnivorous and thus feed on mobile food sources, creating the challenge of designing a food patch that attracts such foragers with controllable initial resource availability and measurable GUD. One way around this is to replicate

the foraging patches but exclude the foragers such that average prey availability in that patch type is used as initial density (Alofs & Polivka, 2004; Polivka, 2007). As mentioned above, this also allows the researcher to account for among-patch variability in initial food density. Likewise, there may be a challenge in designing studies that target planktivores or piscivores that feed from the water column. While not impossible, this also may pose a significant challenge.

2.2.2 | Condition-dependent foraging and predation risk

Because GUD experiments can identify the non-lethal effects of predators on habitat selection, growth, movement, or other behaviours, they affect fitness-correlated traits such as individual condition. Condition affects the perceived level of predation risk and therefore warrants consideration when addressing conservation questions involving the impact of predators on a species of concern. One resultant behaviour is described by the "asset protection principle" (Clark, 1994). Asset protection consists of risk-averse behaviour in which individuals in low condition will take risks and can increase in condition (leaving relatively lower GUDs in risky habitats); however, individuals in good condition take fewer risks and do not make rapid gains in condition (and have high GUDs in risky habitats). The rapid increase in condition by those risk-prone individuals relative to those that start in high condition and take fewer foraging risks can be predicted to cause individuals to converge in their relative condition (Conrad et al., 2011; Luttbeg & Sih, 2010; Sih et al., 2015), thus requiring similar energetic needs and anti-predator vigilance (Olsson et al., 2002; Matassa & Trussell, 2014; Figure 1f). The result is lower among-individual variability in a given measure of condition where predation risk is high compared with less risky habitats (Polivka, 2011).

When it is possible to apply GUDs, quantifying changes in the forager's behaviour in terms of its condition-dependent acceptance of risk with changing predator regimes may be of management interest when intervention with predators is a strategy under consideration. Among-individual variation in growth and condition found in GUD experiments/estimates evaluated asset protection behaviour in sculpins (Cottidae) in both estuarine (Alofs & Polivka, 2004; Polivka, 2007, 2011) and littoral zone lake habitats (Polivka, 2011; Polivka et al., 2013). Condition-dependent movement of roach (*Rutilus rutilus*, Cyprinidae) between a lake and associated streams are modulated by predation risk and asset protection behaviour (Brodersen et al., 2008). Moreover, there is both laboratory (Reinhardt & Healey, 1999) and conceptual (Conrad et al., 2011; Reinhardt, 2002) support for asset protection behaviour in stream salmonids and other fishes (Luttbeg & Sih, 2010). Although it is most robust to conduct GUD experiments to establish the link between anti-predator behaviours and reduced among-individual variability in condition, thus leading to the inference of asset protection behaviour, GUD experiments are not always tractable in aquatic systems. Nevertheless, one may infer such behaviours by evaluating among-individual condition variability for convergence or divergence in a species of concern if its habitats have varying predation regimes (Polivka, 2011, 2020). Therefore, managers with an understanding of the asset protection principle may be able to use the measurement of among-individual variation in body condition to assess relative predation risk. Condition differences among individuals may have consequences for survivorship or other demographic traits.

2.3 | Habitat selection

The biotic and abiotic processes impacting where fish live are fundamental to fish ecology. Habitat selection behaviours can be studied to address conservation and management questions such as what habitat characteristics support healthy fish populations? Which habitats should be restored or protected? How does competition for space within or between species influence habitat selection? Although many studies report correlations between fish distribution/abundance and habitat characteristics (Clarkson & Beseres Pollack, 2021; Smith et al., 2016), which can describe in some detail the habitat requirements of single species or multi-species assemblages (Claudet et al., 2006; Fulton et al., 2020; Marsh-Matthews & Matthews, 2000; Perry & Smith, 1994), they are generally non-mechanistic and results can have ambiguities (Polivka et al., 2015). Nevertheless, below we show how distribution and abundance data can be combined with more mechanistic tools from behavioural ecology. Moreover, other mechanistic models are available, including Ecospace and Ecopath with Ecosim (Christensen & Walters, 2004; Colléter et al., 2015; Heymans et al., 2016), that incorporate bioenergetic inputs and food web structure to identify effects of harvest and location of protected areas. Behavioural theories also provide mechanistic approaches such as the inclusion of population dynamics and density-dependent factors that influence habitat selection. Here we discuss habitat selection theory and its application in predicting distributional patterns based on tradeoffs between resources (food, refuge, and reproduction) and costs (metabolic, competition, or predation).

2.3.1 | Mechanistic approaches to density-dependent habitat selection

Early conceptual development of the relationship between habitat selection and fitness used fish as the study organisms (Gilliam & Fraser, 1987; Werner & Gilliam, 1984; Werner & Hall, 1988), with the subsequent application (e.g., Lindberg et al., 2006), and predicted the minimization of the ratio of density-dependent factors mortality (μ) to growth (g). Density-dependent habitat selection is further described by the "ideal free distribution" (IFD, Fretwell & Lucas Jr., 1969) and the habitat matching rule. An IFD is an equilibrium distribution between habitats that minimizes intraspecific competition for space. The habitat or resource matching rule uses consumer-resource theory to predict that organisms will distribute themselves

in proportion to the resources available to them (Fagen, 1987; Morris, 1994; Parker, 1978). Thus, habitats rich in resources will support higher densities (Niu et al., 2019; Polivka, 2005). These general concepts describe how fish can thus distribute themselves and "vote" with their fins, allowing their relative densities to reflect the productivity of each occupied habitat.

Imagine a fish that occupies two main habitat types. Managers can monitor these habitats for fish density over time as it varies with population size. If distribution across the two habitats follows the IFD, then the relative densities of individuals in each habitat should reach an equilibrium at which fitness is assumed to be equal and the number of individuals in each habitat is reflective of habitat quality (Morris, 1988, 1989). A plot of the relative densities in each can be used to create a usually linear plot known as the isodar ("iso" = equal, "dar" = Darwinian fitness; Figure 2a). The assumption of equal fitness is based on the IFD described above where habitat selection is density-dependent and habitat settlement proceeds according to habitat quality for any given total density of individuals. According to the IFD, individuals are free to move within heterogeneous environments with few to no costs (Hakoyama & Iguchi, 2001; Wagner & Grossman, 2013). The highest quality habitats are settled first and species density in each habitat should reach an equilibrium distribution in each habitat proportional to the relative availability of a key resource in each habitat, that is, productivity (Fretwell & Lucas Jr., 1969). However, there are likely costs associated with habitat selection. As such, there are many examples of why the IFD may not be seen in the field (Tootell & Steele, 2016; Tyler & Gilliam, 1995; Tyler & Hargrove, 1997), including heterogeneous habitats (sand patches among reefs) preventing movement (Chapman & Kramer, 2000; DiFiore et al., 2019), currents and other environmental factors (Shepherd & Litvak, 2004). Therefore, managers must also consider other reasons why fishes are choosing habitats, which may include competition, predation, or other complex interactions.

Figure 2a shows how the slope and intercept of the isodar indicate habitat quality in a study system with respect to habitat degradation or restoration. If the intercept is zero, the two habitats are qualitatively similar, and both begin to be settled at the same time. A positive intercept indicates the preferential settlement of one habitat over another. Similarly, the slope indicates the relative productivity of one habitat over another. A slope = 1 indicates the habitats are qualitatively equivalent and have the same equilibrium density. A slope > 1 indicates that the second habitat is more productive, supports a higher equilibrium density relative to the first and is therefore selected preferentially. Although isodars have been used to evaluate fish habitat selection (Falcy, 2015; Huntsman et al., 2017; Rodríguez, 1995), we know of no case in which they have been used specifically to evaluate fish conservation or restoration (but see Polivka, 2022). We assert that isodars can be used in conservation planning to identify habitats that should be protected or restored and to evaluate the efficacy of those conservation or restoration efforts (Kotler et al., 2016; Morris, 2003).

Fishing/harvesting practices such as bottom trawls or dredges may reduce the productivity of a habitat type (Collie et al., 2017). The isodar approach can be used to track the productivity of habitats as viewed by the fishes themselves. If the cessation of fishing practices corresponds with an increase in habitat productivity, then that habitat can support a higher density of fish which may be reflected in the species' isodar. Conversely, the initiation of a destructive fishing practice would negatively affect the isodar's slope (Figure 2a). Shifts in the isodar may indicate positive responses to fishing practices when a species benefits indirectly (Collie et al., 2017), for example when negative density-dependent (competitive) effects are

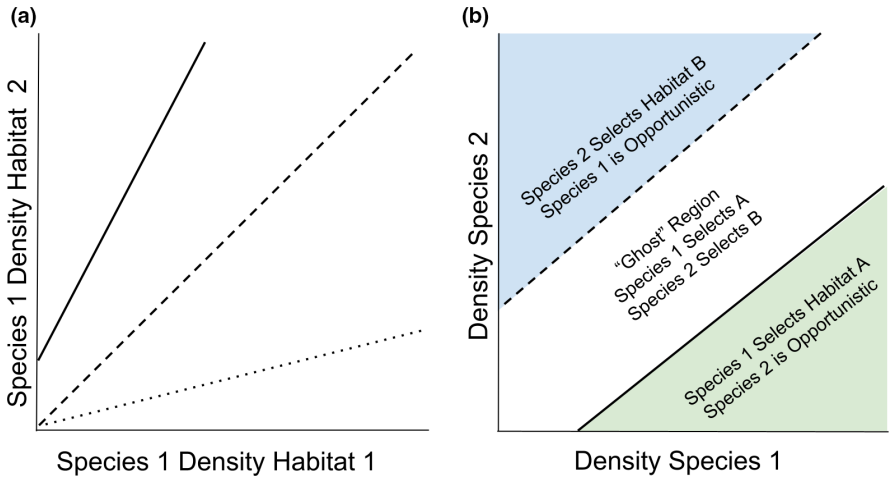

FIGURE 2 (a) Isodar depicting species density in restored (Habitat 1) and unrestored habitats (Habitat 2). The slope of the isodar = 1 (dashed line) indicate an equal preference for both habitats, despite restoration efforts. The slope of the isodar > 1 and a positive *y*-intercept (solid line) indicates restored habitat is selected preferentially across the range of densities observed during the study period. Destructive fishing practices or other habitat degradation in Habitat 2 may result in a shift in the isodar resulting in a slope < 1 (dotted line). (b) Exemplar isolegs depicting densities of two competing species in two habitat types (modified from Morris, 1999; Rosenzweig, 1981). Isolegs for Species 1 (dashed) and 2 (solid) represent population densities at which strategies for habitat selection (selective or opportunistic) are delineated.

alleviated (Hening, 2021). Finally, fine-scale catch and effort data could inform fisheries managers of the relative habitat quality when guided by isodars (van der Lee et al., 2014).

Managers can also use habitat selection theory to understand how interspecific competition may influence a focal species' habitat selection using "isolegs." Similar to isodars, isolegs assess how density-dependent habitat selection occurs in the context of multiple species competing for habitats (Rosenzweig, 1981). Isolegs identify species' unique or shared habitat preferences and can reveal density-dependent selection for habitat specialists and generalists. When plotted simultaneously, isolegs can identify densities where species may co-occur, or completely partition habitats. (Morris, 1999; Morris et al., 2000; Figure 2b). Where complete partitioning is indicated, this range of population densities creates a phenomenon called the "ghost of competition past" (Morris, 1999; Rosenzweig, 1979, 1981, 1991; Figure 2b). However, such a level of partitioning generally means that the focal species does not expand into other available habitats in the absence of the competitor. Thus, isolegs can be used as a tool by managers to show when the removal of a competitor would not result in a redistribution of a focal species into unoccupied habitats. This tool can aid managers in avoiding an ecological trap in which competitor removal alone, as a management action, is unsuccessful and could guide where reintroduction is required in addition to competitor removal (Jeffres & Moyle, 2012; Pelicice & Agostinho, 2008). Finally, Young (2004) used isolegs to analyze the partitioning of habitat by Coho salmon (*Oncorhynchus kisutch*, Salmonidae) and steelhead trout (*Oncorhynchus mykiss*, Salmonidae), two species that are of conservation interest across parts of their ranges and showed the conditions under which strong habitat selection occurs as a result of asymmetric competition.

Although population density data with respect to habitat type are commonly collected, the isodar and isoleg approaches do not take into account the effect of predation on habitat selection or more complex food web interactions. Nevertheless, isodars and isolegs can still provide valuable insights into the habitat use of fishes (see citations above), and the opportunity exists to apply them more frequently to commonly used analytical approaches in fisheries. For example, density dependence quantified at the habitat scale and analyzed with isodars and isolegs can be projected to the whole-population scale via stock-recruitment functions. Additionally, habitat preference calculated from isodar slopes can be used to parameterize the Ecopath with Ecosim Ecospace model (Christensen & Walters, 2004; Colléter et al., 2015; Heymans et al., 2016). This spatially explicit model requires defining the rate of movement into adjacent cells within the habitat map according to habitat preference. Thus, theory can provide a robust input into a commonly used fisheries model to assess management practices and simulated fishing pressure.

2.4 | Movement behaviour

Fish movements among patches, habitats, or across ecotones (e.g., anadromy/catadromy) driven by behaviour or life history processes can be viewed as a mechanism of habitat selection behaviour. Conservation-related changes in fish movements may be associated, for example, with (1) habitat restoration (Irlandi & Crawford, 1997; Polivka, 2020), (2) niches opened by removal of invasive species (Carmona-Catot et al., 2010; Healy et al., 2020; but see Peterson et al., 2004), (3) movement into, or out of, protected areas (Grüss et al., 2011; Pittman et al., 2014), and (4) flight distance of fishes inside or outside protected areas in response to fishing (Bergseth et al., 2015; Januchowski-Hartley et al., 2015). Movements can therefore influence the design and success of conservation efforts.

Movement ecology for the conservation and management of fishes should address whether the effects of either opportunistic or life-history-related movements have increased or maximized fitness (Roberts & Angermeier, 2007). Therefore, complex and often stochastic movement data can be assessed using theory, where internal state or environmental changes should be reflected in the movements of fishes (Nathan et al., 2008). Movements can indicate or depend on the condition of an individual (Heim et al., 2016), and abiotic (i.e., temperature, habitat change; Bergstedt & Bergersen, 1997) or biotic stressors (i.e., predation or competition; Gilliam & Fraser, 2001; Hanson et al., 2007), all of which may relate to conservation efforts. Behaviours can include the frequency and extent of home range movements including foraging, migration distances (Grimm et al., 2017), and diadromy. Variation at the individual level can sometimes be more important than interspecific variation (Harrison et al., 2019). Such an understanding of movement can then be applied to a movement in and out of marine reserves, or smaller-scale movements in and out of restored habitats (Polivka, 2020).

We suggest that descriptive movement studies from micro- to global scales be done in a way that informs managers of the fitness consequences of the studied movement. Mark-recapture (PIT tags, subcutaneous dyes), passive or active telemetry using radio, acoustic or satellite technologies, or downstream trapping of migratory stream fishes (reviewed in Crossin et al., 2017) can indicate habitat affinity and survivorship if the study period is sufficiently long (Stewart et al., 2017). Large-scale life history movements, habitat residence time (via types of resources consumed; Brush et al., 2012; Davis et al., 2018), or migrations can also be tracked using stable isotope analyses from soft tissue or otoliths (Furey et al., 2018). Finally, the energetic costs of movement are quantified by bioenergetic modelling (individual-based models [IBMs], dynamic energy budgets) and may be used to evaluate the physiological implications of movements related to protected or restored habitats (Budy et al., 2011; Hansen et al., 1993; Snyder et al., 2019). These data can then be used to predict fitness-related factors such as survival through life history movements as a result of prey availability (Thompson & Beauchamp, 2016), as well as the status of fish populations and communities (Humston et al., 2004). Finally, the output and predictions from movement behaviour models can inform fishing effort, locating optimal CPUE with explicit spatial data (Alós et al., 2019).

IBMs expand movement patterns that may be measured by managers to evaluate movement behaviour in its adaptive context. IBMs relate fitness to behavioural traits assumed to be adaptive and therefore important to an individual organism's ecological relationships and its ability to optimize fitness (Grimm & Railsback, 2005). IBMs applied in fish ecology focus on habitat characteristics that

are important in movements among habitats according to the trade-off between obtaining energy and avoiding predators (Railsback et al., 1999; Railsback & Harvey, 2002, 2011; see also Section 2.3.1), including how group responses to predators provide social cues that influence individual responses (Herbert-Read et al., 2017). IBMs could also be used in conjunction with GUDs to predict, for example, diet breadth and the spatial scale of foraging movements of fishes (Bianchi et al., 2009; Petty & Grossman, 2010).

FID or minimum approach distance (MAD) are metrics that quantify movement behaviour in response to a perceived, approaching threat (Goetze et al., 2017; Nunes et al., 2015; Ydenberg & Dill, 1986). As such, FID or MAD can serve as a metric of fishing pressure, particularly for spearfishing (Nunes et al., 2018; Samia et al., 2019). More broadly, FIDs are a quantitative tool that can reflect overall fishing pressure. If managers detect FIDs decrease within protected areas (no-take or no-entry), this can indicate the success of protection, or status of recovery (Bergseth et al., 2016; Rhoades et al., 2019) because fish are indicating that risk is relatively lower. Likewise, if managers measure an increase in FIDs in protected areas, this could serve as an indicator that poaching may be occurring in that habitat (Bergseth et al., 2015; Januchowski-Hartley et al., 2012).

Compared to the GUD (Sections 2.2.1 and 2.2.2), FIDs or MADs measure escape or evasion, whereas the GUD measures foraging responses to risk. With this in mind, we must consider the fitness consequences of reduced foraging or increased flight response. If GUDs and FIDs as measures of risk are correlated, then we would predict GUDs to be higher for fish with high FID, and lower with low FID (comparative studies are needed, however). Additionally, costs associated with risk may differ among GUDs and FIDs based on focal species, predator type, or anti-predator strategies. If a manager is interested in measuring human-induced risk, the FID or MAD may be the best approach, whereas if the interest is in quantifying perceived risk from non-human predators the GUD may be the most accessible approach.

Practitioners should also consider aspects of these movement responses to the immediate threat of an approaching human that may be counter-intuitive. Some species may habituate to human presence, and therefore may not display increased FID responses to the "threat" of human presence (as was observed in a terrestrial system with high tourist activity; Tadesse & Kotler, 2012). Likewise, fishes may benefit from the "human shield" effect, in which human presence decreases the risk of predation by predator displacement, resulting in boldness with decreased FIDs (Berger, 2007; Geffroy et al., 2015). As such, FIDs and MADs offer valuable insights into how species respond to risk with movement, but these behavioural responses may differ based on the costs and benefits to the focal species of concern.

Measurement of site fidelity is another quantitative tool that can inform the conservation and management of fishes because lack of movement may exist at one end of the continuum of movement behaviours or maybe a distinct phenotype within a species (such as resident rainbow trout versus anadromous steelhead (*Oncorhynchus mykiss*, Salmonidae)) that can indicate the importance of certain habitats. One theoretical construct for describing the limited movement of fishes is the restricted movement paradigm (RMP), originally applied to stream fishes that commonly showed site fidelity, and for which movement can be costly (Gerking, 1959; Gowan et al., 1994). Indeed, turnover or displacement of individuals can indicate relative habitat quality, and therefore is an informative parameter to evaluate restoration efforts (Chase et al., 2013; Hrenchuk et al., 2017; Rodríguez, 2002). However, mark-recapture studies may be biased toward quantifying individuals that remain in a given location, failing to document longer movements by individuals and thereby giving excess support to the RMP (Gowan et al., 1994).

Site fidelity is well-documented in fish with regard to habitats offering (1) refuge from environmental conditions (e.g., tidepools; Polivka & Chotkowski, 1998; Yoshiyama et al., 1992), (2) breeding sites, for example, in salmon (Salmonidae) (Dittman & Quinn, 1996; Quinn, 1993), and (3) overwintering refugia (Johnson et al., 2015), or (4) specific food resources (Gannon et al., 2015; Zagars et al., 2012). Such habitats may be of importance to conservation efforts, and we believe that there is room for the development and incorporation of behavioural theory and the application of that theory in movement ecology. For example, the RMP can be used to determine the efficacy of restoration efforts based on fidelity to areas of conservation interest (Bronte et al., 2007; Espinoza et al., 2011; Gowan et al., 1994; Polivka, 2020; Teo & Able, 2003). Although commonly applied in fluvial systems, RMP can be applied to marine fishes that exhibit site fidelity of some kind.

Another example in which theory can complement descriptive movement studies is in the identification of essential fish habitats (Kimirei et al., 2013; Sackett et al., 2008). Consideration of fitness can aid the assessment of spawning locations and can identify other critical areas for protection (Stump et al., 2017). Long-term monitoring or suitable reference (non-impacted) populations and/or sites often enable the identification of a mechanistic link between movement responses and positive responses to conservation actions. Finally, movement ecology is often interdisciplinary (Cooke et al., 2008), linking behaviour, physiology, diet, habitat selection, and environmental change.

2.5 | Social behaviours

Many fishes, especially those of economic concern, live in groups, shoals, or schools and exhibit complex social behaviours. In the social context, foraging, habitat occupancy, and reproduction may have different fitness implications for different individuals in the group, depending on how social dynamics drive behavioural variation. Thus, social context and interactions between and within species may provide managers with valuable information on the conditions in place or on the potential effects of management action. Individuals within shoals or schools must balance the tradeoffs of group living: maximizing benefits while minimizing the cost of increased competition. A few of the benefits to individuals living in social groups include increased foraging rates via information sharing, manifested for example, by the producer-scrounger effect, and reduced predation

rates (Giraldeau & Caraco, 2018; Ioannou et al., 2011; Larsson, 2012). These complex behaviours often depend on the state of individuals, the environmental or ecological context, and even fisheries practices (Ginnaw et al., 2020; Ioannou et al., 2011; Rodriguez-Pinto et al., 2020; Sbragaglia et al., 2021). Fishing practices and fisheries management influence socially learned behaviours, such as hook avoidance (Lovén Wallerius et al., 2020). Finally, social learning plays an important role in many fish species and management may benefit from a better understanding of such behaviours (Brown & Laland, 2003). As the mechanisms driving social behaviour in fishes are vast, we do not consider the examples discussed here to be comprehensive.

In our toolkit, we focus on social behaviours with a strong theoretical basis that can be easily monitored and therefore incorporated into management practices. Specifically, shoaling or schooling behaviours are often quantified via visual or acoustic surveys, allowing for the estimation of group size and for the tracking of individuals within a group or population (Mitsunaga et al., 2013; Trygonis et al., 2016; also see Section 2.4), facilitating measurement of key response variables related to certain social interactions. Social network analysis also monitors individual interactions within a group and has been applied to fish shoaling and schooling behavior (see Villegas-Ríos et al., 2022). In previous sections, we introduced the importance of social behaviours (specifically group dynamics) and their influence on foraging, patch use, and movement (see Sections 2.2 and 2.4). Here, we give a specific theoretical application for foraging group dynamics. We then focus on contest behaviours relating to territoriality.

2.5.1 | Group dynamics

Here, we propose the application of theoretical tools to understand how social behaviours in groups may indicate environmental attributes that might be of management interest. Decisions to join groups may be driven by individual interactions (Sumpter, 2010). These interactions result in complex group dynamics and those dynamics are conversely affected by group size. Group dynamics generally reflect the fitness payoffs to individuals in the group and game theory relates such social behaviours with fitness (Maynard Smith, 1974). One tool from game theory, the producer-scrounger game, can predict when species of conservation and management interest can obtain increased foraging opportunities or increased anti-predator vigilance as the result of behaviour within social groups.

In a producer-scrounger game, the "producers" make the behavioural investment in obtaining the resource through active searching and "scroungers" are then able to exploit that resource after it is found by the producer, with the lower effort invested (Barnard & Sibly, 1981; Phillips et al., 2018). The frequency of each of these behaviours in a population should depend on the patchiness of resources (Giraldeau & Caraco, 2018; Morand-Ferron & Giraldeau, 2010). In a study of sticklebacks, large resource patches favoured the scrounger strategy, whereas small resource patches favoured individual foraging (Hansen et al., 2016). In Coho salmon (*Oncorhynchus kisutch*, Salmonidae), body size can affect the outcome of each strategy. Small individuals are often producers and larger ones are predicted to be scroungers in a model built from this study system. This model also showed that as group size increased, so did the equilibrium frequency of scroungers in the group (Phillips et al., 2018). These equilibrium frequencies can put overall limits on total group size and thus population size (Niwa, 1998), or even the individual's decision to join a group at all (Niwa, 2003, 2004) because the total food obtained by the group as a whole may decrease as the relative frequency of scroungers increases (Phillips et al., 2018). In species known to have producer-scrounger dynamics while foraging as groups, the number and size of groups can indicate food availability to species of concern.

Managers interested in social foraging species may use group size, the number of groups, and the size distribution of individuals within a group as an indicator of population status or as a tool to evaluate conservation and management strategies. Larger or more numerous groups may indicate larger populations (Brierley & Cox, 2015; Furuichi et al., 2022; Holubová et al., 2019) or the presence of predators leading to anti-predator vigilance via larger groups (Herbert-Read et al., 2017; see also Section 2.2.1). If the driver of this density-dependent relationship between the group and population size is the producer-scrounger game, in at least some species, we expect a higher proportion of large individuals (scroungers) as populations increase (Hansen et al., 2016; Phillips et al., 2018). Thus, estimation of fish size in groups of social foragers, data that are relatively easy to obtain, even visually, may serve as an effective approach to monitor populations of conservation concern. Likewise, managers may evaluate conservation actions, such as food enhancement/supplementation, that target species with producer-scrounger dynamics. In such species, food enhancement should increase group foraging over individual foraging (Hansen et al., 2016), with positive implications for populations. The relationship between grouping behaviour and population size in social foraging species (Brierley & Cox, 2015; Furuichi et al., 2022; Holubová et al., 2019), implies that such an observation can connect food enhancement with an increasing fish population. To employ the producer-scrounger game as a tool, managers should first consider whether social foraging is the primary driver of grouping behaviours for species of concern. The detailed computational principles behind the producer-scrounger game are outside the scope of many management approaches, but the general predictions about group size and dynamics may still be valuable in monitoring populations for stability or trends over time. As a final caveat, further studies are needed to test the relationship between group size and population size, and its strength, in wild fish populations (Hensor et al., 2005).

Contest behaviours are social behaviours that may result from group interactions (Briffa & Sneddon, 2010). Individual contests within social groups can yield insight into competition for specific resources such as food, territories, or mates. Again, game theory provides an analytical tool for these contests, namely in the form of the classic "hawk-dove" game (Maynard Smith & Price, 1973)

with current applications in fish ecology (Paijmans & Wong, 2017). Fitness is determined by the relative costs and benefits of competing/fighting ("hawk") or retreating ("dove") and the environment may determine what level of competitive behaviour may be optimal. In a resource-poor environment, each unit of available resource is valuable which should lead to more frequent and/or intense contests, possibly favouring the "hawk." Conversely, resource-rich habitats should have a lower number of bouts or duration of contests. Although the "hawk" or "dove" strategy might be genetic or morphological traits with fixed frequencies (Maynard Smith & Price, 1973; Paijmans & Wong, 2017), especially when linked to body size (Reddon et al., 2011), switching strategies depending on availability of resources may be favoured and lead to plastic phenotypes (de Lourdes Ruiz-Gomez et al., 2008; Gunn et al., 2022). Therefore, managers can exploit these behavioural responses as an immediate reflection of conditions in place from a fish's point of view.

Monitoring contest behaviours are useful because measurement of territory size, and the number and/or duration of contest bouts may reveal habitat quality from the perspective of a species of conservation concern. Such observations are relatively straightforward with field video recording. These behaviours may provide a data-driven approach to conservation, depending on the needs of the practitioners. High frequency or duration of contest behaviours or large territory sizes may reflect low habitat quality, directing managers to regions in need of restoration. Conversely, low frequency or duration of contest behaviours or small territory sizes may reflect high habitat quality, thereby identifying regions for protection. Such predictions from the hawk-dove game are supported in field studies (Berumen et al., 2005; Keith et al., 2018; Samways, 2005), but have yet to be applied to adaptive management plans.

3 | SUMMARY AND PROSPECTUS

3.1 | Summary

The theoretical concepts we described here comprise a behavioural ecology toolkit (Figure 3) that practitioners may incorporate into their conservation and management strategies. This toolkit provides both novel and complementary approaches to current assessment strategies or conservation efficacy studies. Foremost, behavioural theory allows practitioners to address conservation goals with testable hypotheses. The range of conservation questions makes it relatively straightforward to identify opportunities to employ one or more of the conceptual approaches for application to fish conservation and management (Figure 4). Linkages between concepts and methodologies can direct managers to innovative study designs and ways of interpreting data that potentially generate conclusions

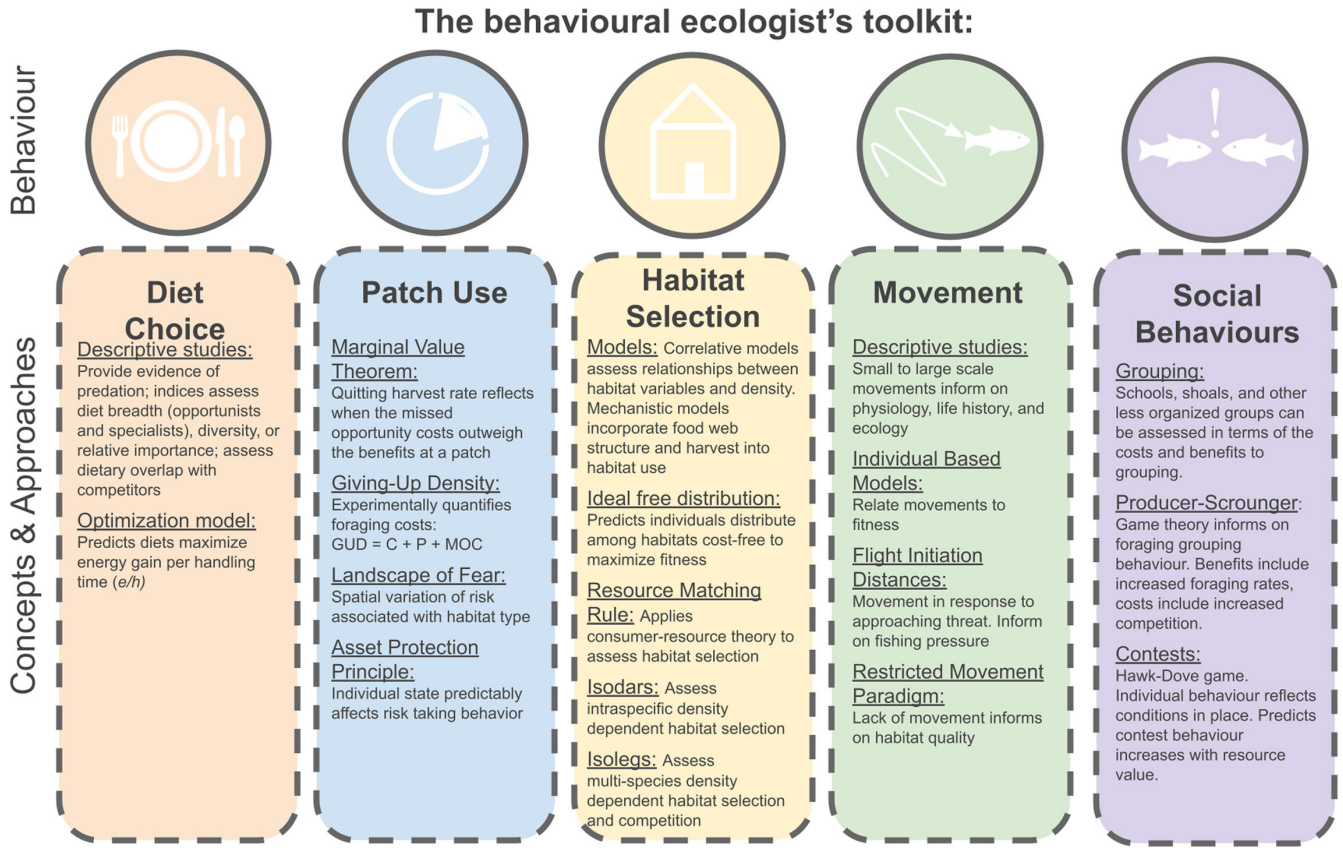

FIGURE 3 The behavioural ecologist's toolkit for fish conservation and management. We identify 5 behaviours, diet choice, patch use, habitat selection, movement, and social behaviours and their associated concepts and approaches for application to fish conservation studies.

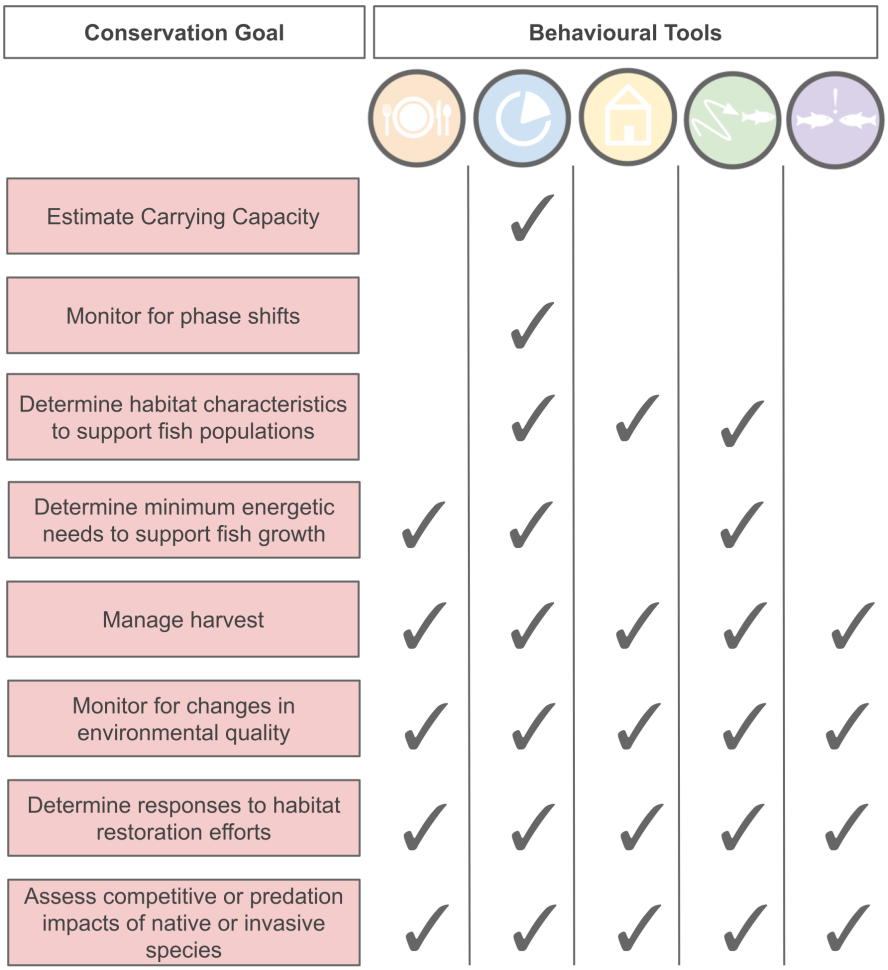

FIGURE 4 Conceptual diagram linking goals for the conservation and management of fishes to behaviours, diet choice, patch use, habitat selection, movement, and social behaviours. Many conservation goals can be addressed through the application of multiple behavioural approaches.

with mechanistic detail. Furthermore, we specify approaches that are applicable to research questions at multiple scales or those with a non-intuitive application in freshwater or marine systems. Finally, the theoretical constructs we discussed make specific predictions for the range of possible behavioural responses to environmental factors such as predation risk, conspecific cues, and resource or habitat availability in which the responses may be shaped by natural selection.

3.2 | Prospectus

To implement the behavioural toolkit to questions in the conservation of fishes, managers should first determine the behaviours appropriate to answer those questions and connect them to the relevant concepts using Figures 3 and 4 as a guide. Common strategies for fish conservation and management include establishing protected areas, habitat enhancement, the opening and closing of fisheries, aquaculture, and stocking. Measurement of subsequent behavioural changes using concepts from the toolkit can therefore inform adaptive management strategies by identifying the underlying mechanisms that drive population change (Parma, 1998; Rilov et al., 2019). Additionally, because these behaviours are shaped by natural selection and linked to fitness, we should also consider how fisheries management may serve as a selective force on these and other behaviours, and thereby fish populations (Jørgensen et al., 2007; Sbragaglia et al., 2021).

The behavioural toolkit can be used as a framework to assess data in new ways or to supplement current approaches for evaluating the conservation and management of fishes. For example, to determine whether habitat restoration has increased habitat quality, time series of fish density data are commonly collected (Figure 4). Thus, the use of isodars can evaluate preference for restored habitat over a range of total density (Figure 2). Likewise, when dietary data are collected before and after a conservation action, they should be analysed, not only for changes in consumption but also under the hypotheses of optimal diet theory described above (see Section 2.1). When the management action may affect intra- or interspecific contests, managers should plan observations of agonistic behaviours, which are hypothesized to decrease as habitat quality increases. Finally, we suggest patch use behaviour experiments to reveal any non-lethal effects of predators that follow target species to enhanced habitats. Changes in habitat quality may modulate energetic gains and identify potential ecological traps due to conservation or restoration (Jeffres & Moyle, 2012).

Common modelling approaches used in fish conservation and management may also benefit from the behavioural toolkit. For example, bioenergetic models predict fish responses to food availability and habitat conditions in terms of energetic consumption and

growth. Although more aligned with physiology than behavioural ecology, when combined with the behavioural toolkit (e.g., multi-trophic level data on diet choice and optimal diet choice theory), these models can estimate an individual's success when food web pathways are affected by conservation or restoration actions (e.g., Bellmore et al., 2017; Benjamin et al., 2020). In particular, conservation actions such as food augmentation cause detectable, although temporary, responses in bioenergetic models (Benjamin et al., 2020; Rosenfeld et al., 2005) if foragers become more selective or more generalist in response. The combined approach of bioenergetic modelling and optimal diet choice behaviours can estimate consumption rates of target species by top predators (Beaudreau & Essington, 2009; Mesa et al., 2013), which may be of importance when species recovery efforts incorporate predator management.

Often managers already have a management strategy but are looking for new tools to complement current approaches. Given limitations of time, personnel, and budgets, not all approaches may be available in every case, but efficient means of allocating study resources to these methods should be considered. In particular, we envision patch use behaviour has the potential for broad application in the field of fish conservation and management, as it can serve as an indicator of the status of individuals, populations, and communities. Finally, with a behavioural framework in mind, managers may find they have a wealth of data at their fingertips to interpret in new ways, including analysis of commonly collected data on distribution and abundance. Ultimately, there are multiple pathways to gain insight into how conservation actions might affect fitness, and thereby population status of fish species of concern (Figure 3).

3.3 | Broader context: Fitness implications

The behavioural ecology toolkit places behavioural variation among individuals in a context of natural selection driven by environmental quality, or even fishing practices (Claireaux et al., 2018; Sih et al., 2012). The methods we presented in this review generally make predictions with the underlying assumption that individuals are behaving optimally, but there may be cases when optimal behaviour is not occurring. For example, patch use experiments may not indicate a perfect trade-off between foraging and predation risk, but may suggest a more risk-reckless strategy (Alofs & Polivka, 2004). Nevertheless, behavioural ecology provides the quantitative and mechanistic links between behaviour and fitness. Thus, the application of these methods to the conservation biology of fishes will likely increase the confidence managers have in conclusions made about the efficacy of conservation efforts. Whereas behavioural variation in response to environmental change has been studied, habitat selection, density-dependent movement, diet, foraging behaviour, patch use, and asset protection all measure potential correlates of fitness and/or are compatible with other existing models that have management applications. Thus, behavioural ecology reveals the link between behaviour and fitness, providing a mechanistic explanation for the diversity of phenotypes maintained in a species or population (Mangel & Stamps, 2001; Mittelbach et al., 2014; Stamps, 2007). Such diversity may be a desirable outcome of management efforts. This behavioural ecology toolkit may identify benefits of conservation efforts that might not otherwise be apparent.

4 | CONCLUSION

The conservation and management of fishes have the unique challenge of conserving species as a resource for commercial, recreational, and subsistence fisheries, as well as for promoting ecosystem function and biodiversity. Fisheries managers can use the behavioural ecology toolkit to assess the efficacy of their conservation efforts. This theory-driven approach allows for testable hypotheses and predictions at multiple scales. Additionally, managers can interpret specific fish responses using the foundational concepts of behavioural ecology, thereby informing management strategies. Finally, we propose that the training of natural resource specialists and conservation agency biologists be complemented with theories and methodologies obtained from behavioural ecology. Uniting fisheries management and behavioural ecology should elevate the certainty about the potential success of fish conservation programs.

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CONFLICT OF INTEREST

The authors have no conflicts of interest related to this manuscript

DATA AVAILABILITY STATEMENT

No original data were produced for this study.

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