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What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants

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Abstract

Considerable time and money are expended in the pursuit of catching fish with hooks (e.g., handlining, angling, longlining, trolling, drumlining) across the recreational, commercial and subsistence fishing sectors. The fish and other aquatic organisms (e.g., squid) that are captured are not a random sample of the population because external (e.g., turbidity) and underlying internal variables (e.g., morphology) contribute to variation in vulnerability to hooks. Vulnerability is the probability of capture for any given fish in a given location at a given time and mechanistically explains the population-level catchability coefficient, which is a fundamental and usually time-varying (i.e., dynamic) variable in fisheries science and stock assessment. The mechanistic drivers of individual vulnerability to capture are thus of interest to fishers by affecting catch rates, but are also of considerable importance to fisheries managers whenever hook-and-line-generated data contribute to stock assessments. In this paper, individual vulnerability to hooks is conceptualized as a dynamic state, in which individual fish switch between vulnerable and invulnerable states as a function of three interdependent key processes: an individual fish's internal state, its encounter with the gear, and the characteristics of the encountered gear. We develop a new conceptual framework of "vulnerability," summarize the major drivers of fish vulnerability, and conclude that fish vulnerability involves complex processes. To understand vulnerability, a shift to interdisciplinary research and the integration of ecophysiology, fish ecology, fisheries ecology and human movement ecology, facilitated by new technological developments, is required.

KEYWORDS
angling, catchability, exploitation, fisheries management, longlining, state switching

1 | INTRODUCTION

Human populations are generally densest near shores of oceans, estuaries, lakes and rivers that provide access to water and related biological resources. Among the most prominent of these resources are aquatic animals, which are exploited in commercial, recreational and subsistence fisheries for consumption and pleasure. Humans have fished since the origin of the species (Radcliffe, 1921) and fishing continues to be central in many societies and economies. Regardless of whether fishing is practiced for commercial gain, personal consumption or pleasure, capturing animals is crucial to all fishers and fisheries sectors. The importance placed by humans on fishing and the desire to catch either large numbers or individuals of large size (e.g., Arlinghaus, Beardmore, Riepe, Meyerhoff, & Pagel, 2014) has also led

to rapidly advancing technology for fishing in both commercial and recreational fisheries (von Brandt, 1984). Any gear is to some degree selective for certain traits of the fish (Ricker, 1969). Thus, fishing is a non-random process, and some species or individuals within a given species are more likely to be captured than others (Lewin, Arlinghaus, & Mehner, 2006). Experienced fishers recognize this fact and they attempt to alter their fishing behaviour to increase the probability of catching specific species, sizes or even individuals to satisfy their personal goals.

Success in fishing can be described as an extension of a predator-prey dynamic, which depends on the ability of people (predators) to encounter and capture fish (prey; Post, Persson, Parkinson, & Kooten, 2008). Cox and Walters (2002) and Walters and Martell (2004) conceptualized dynamic differences in vulnerability of a prey population to predators within foraging arena theory (for an application to a largemouth bass, *Micropterus salmoides*, Centrarchidae, recreational fishery, see Matthias, Allen, Ahrens, Beard, & Kerns, 2014; for a review, see Ahrens, Walters, & Christensen, 2012). Accordingly, in any moment in time some fish are in vulnerable states while others are invulnerable. Individuals move between these states at some unknown rate. In classical foraging arena theory, the invulnerable pool of fishes usually hides in refuges where they are not accessible to predators. However, in a fishing context, invulnerability must not be confined to spatial inaccessibility because there can be many traits that render certain individuals invulnerable to hooks (e.g., variation in aggression; Sutter et al., 2012). In fact, the exchange rate between vulnerable and invulnerable states can also be conceptualized to constitute a trait upon which selection acts. Accordingly, not all individuals from a species or population are equally vulnerable to exploitation by fisheries (Miller, 1957; Anderson & LeRoy Heman, 1969; Beukema, 1970a, 1970b; Hackney & Linkous, 1978; Raat, 1985; Katano, 2009; Klefoth, Pieterek, & Arlinghaus, 2013), suggesting the potential for a genetic basis to vulnerability to fishing (Klefoth et al., 2013; Philipp et al., 2009; Wohlfarth, Moav, Hulata, & Beiles, 1975). Vulnerability, the probability of a single fish being captured by a specific fishing gear, is thus an individual phenotype upon which fisheries selection acts (Uusi-Heikkilä, Wolter, Klefoth, & Arlinghaus, 2008). Vulnerability is a complex trait composed of or correlated with a range of physiological, behavioural, morphological and life history phenotypes (Uusi-Heikkilä et al., 2008) and it is strongly influenced by phenotypic plasticity (e.g., learning) and ecological conditions (e.g., nutrients and relatedly hunger; Løkkeborg, Siikavuopio, Humborstad, Utne-Palm, & Ferter, 2014). Vulnerability is polymorphic within a stock, hierarchically structured (i.e., some of its components induce a cascade of events) and is comprised of nonlinear responses to a range of environmental stimuli (i.e., vulnerability in many species nonlinearly decreases with increasing fishing effort; Alós, Palmer, Trias, Diaz-Gil, & Arlinghaus, 2015; Alós, Puiggrós et al., 2015). Cumulatively across all individuals, the individual vulnerability drives dynamic population-level catchabilities and ultimately the catches and harvesting efficiency.

The catchability coefficient is a key population-scale metric used in stock assessment that relates the biomass of a wild fish stock to the capture or fishing mortality, reflecting the efficiency of a given fishery (Arreguín-Sánchez, 1996). Catchability is time-varying (Die, Kell, & Pallares, 2002; Peterman & Steer, 1981; Wilberg, Thorson, Linton, & Berkson, 2009), reflecting variation in vulnerability of fishes to fishing gear (e.g., across seasons), but a comprehensive mechanistic approach to vulnerability of individual fishes to fishing gear has not been established. Fully understanding the processes contributing to fish capture can contribute to advancing many aspects of fish exploitation and fisheries management. Although fishing activities are extremely diverse, we restrict the scope of our article to hook and line fishing, which includes fishing with rod and reel or handlining as in many recreational and subsistence fisheries as well as use of longlines and drum lines, practiced by many commercial fishing operations. Hook and line fishing (fishing, hereafter) is generally characterized by terminal hooks extending from a length of line (e.g., monofilament) attached to a rod and a reel, simple spool (i.e., handlining), drum or a longline. The terminal hooks are baited with natural baits or artificial baits/lures intended to incite feeding or aggression (which may lead a fish to strike but not consume) that results in retention of the hook and ideally capture of the fish. Unlike other fishing gears that either passively collect fish (e.g., gill net) or those that actively capture fish (e.g., trawl net, seine net), no matter if a hook is present, the fish must make a decision as to whether it will bite or not (Løkkeborg et al., 2014). Hence, the importance of fish behaviour is particularly high in the capture process by hooks.

Quantifying vulnerability of fish to hook and line fishing gears requires an integrated understanding of fish behaviour, physiology, morphology and cognition, as well as an appreciation of the controlling influence of external variables such as the abiotic environment, social contexts and the fishery (gear type, harvest regulations). Exploring how and why fish become vulnerable to fisheries can make significant contributions to the fundamental understanding of fish ecology within an exploited system. Such understanding will also be of interest to fishers and anglers by helping to understand variation in catch and by-catch rates. Knowledge of how and why fish are captured in fisheries is essential for developing applied conservation strategies and management plans for sustainable use of aquatic resources. Many studies have provided insight into the mechanisms that influence fish movement and feeding, which can be interpreted from the perspective of fishing vulnerability and applied to a mechanistic framework on the capture of fish by fishers. In doing so, we demonstrate how fish vulnerability can be viewed as a dynamic state-switching process between vulnerable and invulnerable states, and based on this notion we develop a conceptual framework for studying fish vulnerability to hooks in this paper. In addition, we present a comprehensive review of scientific literature that supports a mechanistic understanding of fish vulnerability to fisheries. Considering that hook-related gear is common in both freshwater and marine systems (Anticamara, Watson, Gelchu, & Pauly, 2011; Arlinghaus, Tillner, & Bork, 2015), our work has implications for the sustainability of global aquatic systems. Our work will also contribute to the desire of many anglers to scientifically understand when, how and why individuals fishes are captured (as in popular literature, e.g., Sosin & Clark, 1973; Johnson, 1984; Kageyama, 1999).

2 | A CONCEPTUAL MODEL OF FISH VULNERABILITY TO HOOKS

To conceptualize the factors affecting fish vulnerability, we propose a framework of individual heterogeneity in vulnerability and the factors that modulate the switching of individual fish from an invulnerable to a vulnerable state (Figure 1). This framework integrates three major mechanistic components that contribute to the probability of a fish being captured by fishing gear: the internal state of the individual, the encounter with fishing gear and the gear and regulation dependent selectivity (Figure 1). All three components are in theory independent and have additive effects. Some of the components have *sine quan non* properties, for example because capture is impossible without encounter with gear. The components are often strongly correlated; for example, a hungry fish is often more exploratory, facilitating the predatory encounter with gear. Our solution to properly address all factors governing vulnerability on an individual scale is to consider capture (vulnerability) as a temporally and spatially explicit process that can be derived from observing the three central components of vulnerability along with the external variables that modulate them (Figure 1).

2.1 | Internal state

Vulnerability of fish to fishing gear is systematically related to a range of potentially correlated external variables such as the abiotic and biotic environments and their interaction with traits such as the morphology, life history, cognition, physiology and movement traits that combine to determine the internal state of the fish (Uusi-Heikkilä et al., 2008). We define the internal state that affects vulnerability as those factors that induce motivation to eat and strike baits or lures. The need to eat is ultimately regulated by the fish's metabolism, which can be genetically based, along with endocrine cues that together control the fluctuation of hunger on short timescales (Einen, Waagan, & Thomassen, 1998) and food availability. Environmental variables control cellular and biochemical processes that contribute to energy fluxes and feeding requirements and therefore a fish's ecophysiology is central to the rate of metabolism and thereby the internal state (Fry, 1971; Figure 1). Although metabolism is also correlated with body size (Schmidt-Nielsen, 1984), the importance of body size is discussed in the context of the gear selectivity because of the relationship between gear, fish size and vulnerability. The life history, physiological, behavioural and morphological traits that collectively induce hunger and the motivation to eat or strike stimulate the transition from the invulnerable to the vulnerable state, or vice versa, which will be strongly affected and driven by the perception of predation risk (Ahrens et al., 2012). Vulnerability to capture by hooks is particularly affected by behavioural decisions of fish in the presence of fishing gear (Alós, Palmer, Rosello, & Arlinghaus, 2016; Härkönen, Hyvärinen, Paappanen, & Vainikka, 2014; Wilson, Binder, McGrath, Cooke, & Godin, 2011; Wilson, Brownscombe, Sullivan, Jain-Schlaepfer, & Cooke, 2015). There is accumulating evidence of consistent and repeatable fish behaviour in fisheries contexts (i.e., personality or behavioural types; Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011; Mittelbach, Ballew, & Kjelvik, 2014). The behavioural components of fishing vulnerability have, therefore, received attention in recent years through the study of animal personality, which has the potential to play a major role in driving the different components

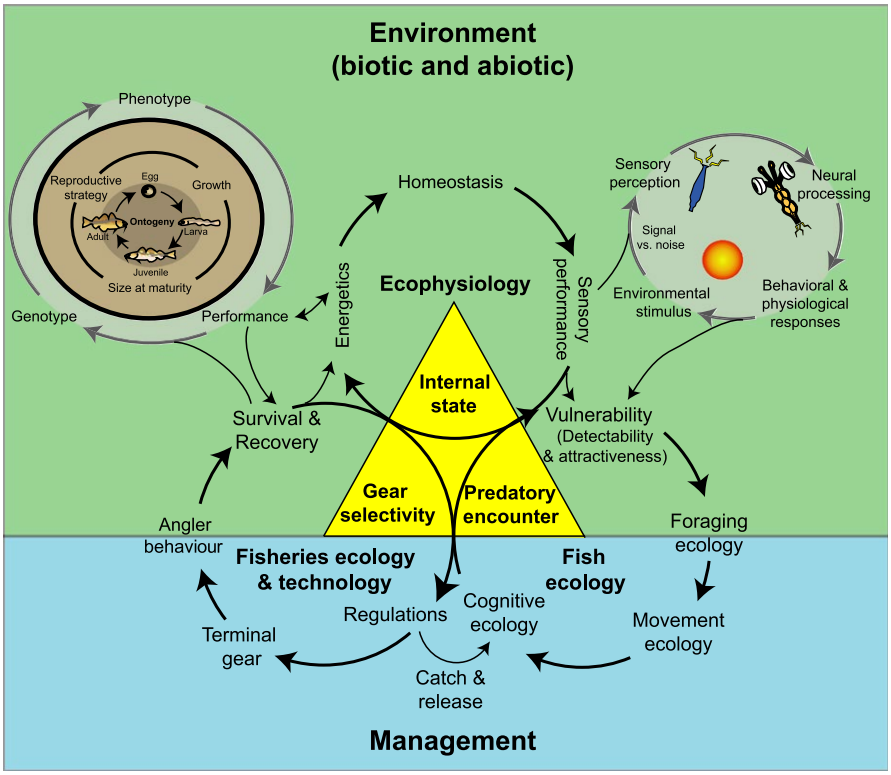

FIGURE 1 Vulnerability of fish conceptualized as a dynamic state-switching process in which fish transition into states of vulnerability as a function of the internal state, the encounter with the predator (i.e., fisher), and the selectivity of the gear. We also show how vulnerability is modified across axes of life history and environments and how it can be modulated by management actions such as fishing restrictions. Fish vulnerability is only observable insofar as the fish is captured, making it difficult to empirically quantify. Nevertheless, these concepts are the foundational mechanisms driving vulnerability. [Colour figure can be viewed at wileyonlinelibrary.com]

of the internal state of the individual (Figure 1). A vulnerable internal state means that the fish is motivated to forage (i.e., take the bait or strike the lure, because of hunger or hunger-independent aggression; Sutter et al., 2012), which is thus the first component of the overall framework proposed here (Figure 1). Details of the mechanisms involved in state changes are expanded on below (see also Figure 2).

2.2 | Encounter

Given an internally vulnerable state (i.e., the fish is motivated to forage), the vulnerability of an individual is a function of the encounter rate with the gear (Figure 1; Alós et al., 2016; Alós, Palmer, & Arlinghaus, 2012). The probability of hooking a fish will thus depend on the spatial and temporal distribution of the gear and the animals (Matthias et al., 2014), modulated by the probability that an individual will strike a hook as well as on the probability that a strike results in hooking and capture (i.e., gear retention; Deriso & Parma, 1987). Encounters are further modulated by the ecology of both the species and individual scales. Encounters with a fish by fishing gear should theoretically increase with the activity of individual fish (Kallayil, Jørgensen, Engås, & Fernö, 2003; Turesson & Brönmark, 2004) and several authors have suggested this relationship (Alós et al., 2016; Ãrnason, Hernandez, & Kristinsson, 2009; Parsons et al., 2011). The science of predator-prey encounters is well developed via the concept of optimal search behaviour (Turesson & Brönmark, 2004; Turesson, Brönmark, & Wolf, 2006) and the emerging unification of fish movement and personality will offer mechanistic explanations of individual variation in encounters (Bartumeus, Catalan, Fulco, Lyra, & Viswanathan, 2002; Bartumeus et al., 2008; Domenici, 2001; MacKenzie & Kiorboe, 1995; Nathan et al., 2008). The study of encounter rates in fishing systems, however, also needs to consider the behavioural patterns of fishers or the variability in the movement patterns of fishing gear (Alós et al., 2016; Matthias et al., 2014). The encounter probability of a fish to gear will depend on both the movement rate of the fisher and gear and the movement rate of the fish, but a more mobile fish should still have a higher probability of encountering the fishing gear compared to less mobile individuals (Alós et al., 2016). At shorter spatial scales, the encounter process is linked to the sensory ecology of the fish and its ability to perceive gear (Klefoth, Skov, Krause, & Arlinghaus, 2012), its cognitive ecology and its capacity to process the gear and interpret it as food (or as risk), and finally its foraging ecology in the context of predation risk (Figure 1). Fish have a variety of strategies for hunting and the encounter is a function of the foraging (i.e., strike and ingestion) behaviour. With rapidly developing tracking tools of fishes (Baktoft et al., 2012; Cooke et al., 2004; Hussey et al., 2015) and humans (i.e., fishers; Gonzalez, Hidalgo, & Barbasi, 2008; Walker, Rivoirard, Gaspar, & Bez, 2014), fish behaviour can now be assessed in the wild, offering opportunities to quantify encounters between fish and fishers. The theories behind the biological encounters cover many disciplines of movement ecology and foraging ecology (including human ecology) and provide a unique opportunity for understanding the spatial component of fishing vulnerability.

2.3 | Gear selectivity

Following the encounter between the internally vulnerable fish and the fishing gear, the gear ultimately determines fate of the fish because any gear is usually selective for morphological traits (Figure 1). The selectivity of gear can also depend on the fish's capacity to learn and remember, for example in catch-and-release fisheries (Beukema, 1970a; van Poorten & Post, 2005; Klefoth et al., 2013; Lennox, Diserud et al., 2016). The selectivity also depends on the physical characteristics of the gear in relation to the fish (Figure 1). In many fishing situations, larger fish are preferentially captured and such size-based exploitation has implications for the sustainability of wild stocks (Jørgensen et al., 2007; Laugen et al., 2014; Palkovacs, 2011). Morphological variables such as gape size limit the possibility of ingestion and capture of certain hook sizes (Erzini, Goncalves, Bentes, & Lino, 1997; Karpouzi & Stergiou, 2003; Millar, 1992). In fact, the link between vulnerability and gear size has already been widely accepted as a management tool to modify exploitation rates in fisheries worldwide (Arlinghaus, Klefoth, Kobler, & Cooke, 2008; Cerdà, Alós, Palmer, Grau, & Riera, 2010; Wilde, Pope, & Durham, 2003). Type, colour or texture of lures also has a role in determining the ultimate vulnerability of an individual to a specific lure type (Alós, Arlinghaus, Palmer, March, & Alvarez, 2009; Alós, Mateu-Vicens, et al., 2009; Hsieh, Huang, Wu, & Chen, 2001; Orsi, Wertheimer, & Jaenicke, 1993; Wilson et al., 2015). Perhaps the most important decision for fishers is the appropriate bait to use in a situation where a vulnerable fish encounters the gear (Figure 1). Research is emerging on whether the bait type consistently affects catch rates in recreational fisheries (Arlinghaus, Alós, Pieterek, & Klefoth, 2017). What is known is that incorrect bait can move an otherwise vulnerable fish back to the invulnerable state. The gear choice therefore constitutes the final step of the vulnerability process suggested here (see Figure 1) and the synergistic study of the internal state, probability of encounter, and the gear effectiveness should effectively predict the final fate of a given fish targeted by a fishery (Figure 1).

3 | REVIEW OF FACTORS UNDERLYING FISH VULNERABILITY

3.1 | Abiotic environment

Environmental quality of potential fishing sites is one of the key factors used by fishers when deciding where to fish (Berman & Kim, 1999; Cabanellas-Reboredo et al., 2014; Hunt, 2005; Jackson & Davies, 1988). The abiotic environment can be divided into the physical (e.g., temperature, light, lunar phase, wind, flow) and the chemical (e.g., dissolved oxygen, pH, salinity) environments, which can modify a fish's internal state and encounter rates with gear (Figure 2; Stoner, 2004). Here, we focus on the effects of temperature, light, lunar phase, flow, wind, barometric pressure and dissolved oxygen on fish vulnerability, mindful that the impacts of the environment on fish are a function of the ecological niche and habitat that the species or population is adapted to. These are the best studied abiotic parameters in the

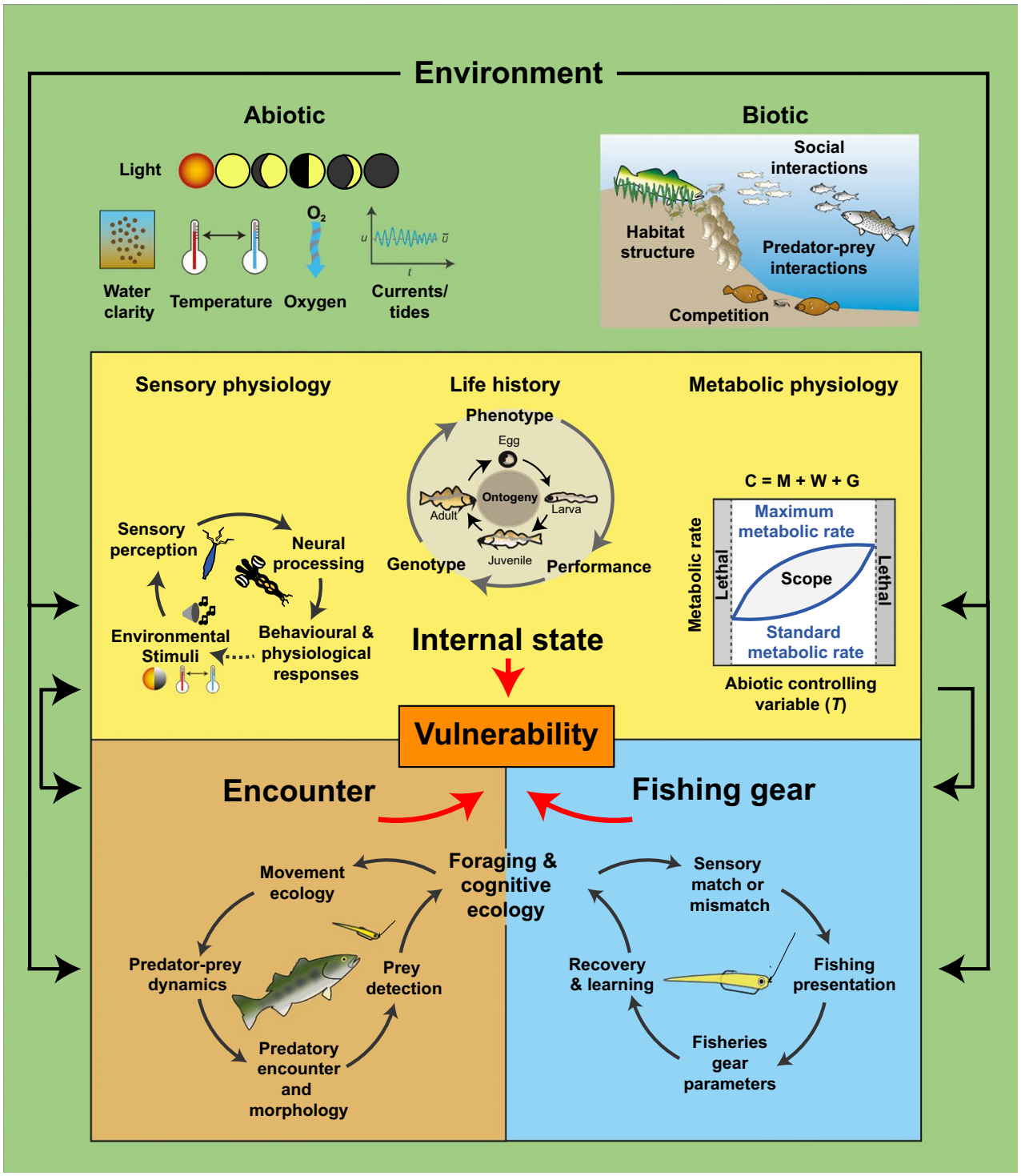

FIGURE 2 In Figure 1, we introduced the concepts of Internal State, Encounter, and Gear and their role in determining individual vulnerability of fish to gear. Here, we illustrate the relationship of crucial topics in vulnerability research within this framework: the abiotic and biotic environments, morphological and life history phenotypes, cognitive and metabolic physiology, movement, sensory and foraging ecology, and fishing gear. These topics further correspond to the sections reviewed in Chapter 3 of this paper: the concepts in fish vulnerability linking internal and external factors that contribute to the probability of individual fish capture, which are described in detail in the main text. Hungry fish are more vulnerable to angling, and probability of hunger is influenced by internal states such as genotypes, physiology, metabolism (i.e., consumption = metabolism + waste excretion + growth) and personality. Hungry fish will seek and encounter food given appropriate environmental conditions and also biotic conditions such as predation risk and social interactions. Detection of gear depends on the movement (of both gear and fisher) and the physiology and morphology of the fish. Selection and consumption of the gear depends on previous learning or conditioning (i.e., whether it is perceived as possible food), which is affected by the fishing gear itself including the shape, colour, scent, size and movement of the gear. The intersection of the internal state, encounter and fishing gear therefore determines the ultimate vulnerability of fish as illustrated in this figure. [Colour figure can be viewed at wileyonlinelibrary.com]

context of fish vulnerability (Table S1). Other aspects of the environment have not been studied in detail; however, suboptimal chemical environments such as those resulting from changes in salinity or pH, for example, result in impairment of behaviours that contribute to vulnerability such as movement or alter the internal state to produce an invulnerable fish (Leduc, Roh, Harvey, & Brown, 2006; Mazeaud, Mazeaud, & Donaldson, 1977; Schulte, 2014).

Water temperature modifies fish behaviours that are related to vulnerability and is perhaps the best-developed environmental variable related to fish vulnerability (Table S1). Temperature alters a fish's activity (Fry, 1971), swimming speed (Videlier & Wardle, 1991; Watz & Piccolo, 2011), jaw mechanics (Devries & Wainwright, 2006; Wintzer & Motta, 2004), metabolism (Brett, 1964; Brett & Glass, 1973), taste preferences (Kasumyan & Døving, 2003) and temporal foraging patterns (Fraser, Metcalfe, & Thorpe, 1993). Most of the effects of temperature on vulnerability are inferred through these changes noted above (Castonguay & Cyr, 1998; Stoner & Sturm, 2004) rather than being studied explicitly in the context of hook and line fisheries. In marine pelagic fisheries, sea surface temperature can predict catch rates (Damalas, Megalofonou, & Apostolopoulou, 2007; Vanderlaan, Hanke, Chassé, & Neilson, 2014), but this is often driven by higher fish densities where temperatures are optimal rather than increased searching and hunger. Vulnerability was negatively related to temperature in northern pike (*Esox lucius*, Esocidae) and rainbow trout (*Oncorhynchus mykiss*, Salmonidae; Casselman, 1978; McMichael & Kaya 1991; Kuparinen, Klefoth, & Arlinghaus, 2010). Reduced vulnerability at high water temperatures likely alters the internal state by inducing physiological stress in the predator or by stimulating prey fish activity, decreasing the likelihood that a predator would notice fishing gear relative to prey.

Light levels affect foraging success and activity (De Robertis, Ryer, Veloza, & Brodeur, 2003; Stoner, 2004; Nilsson et al., 2012; Jönsson et al., 2007; Figure 2; see Sensory ecology section). Accordingly, light availability is a key determinant of peak activity and foraging times in many fish species (Horodysky, Brill, Warrant, Musick, & Latour, 2010; Kuparinen et al., 2010; Reynolds & Casterlin, 1976). The ability to forage requires at least some level of light for most species except for nocturnal/aphotic fishes that forage based on olfaction or other cues (e.g., Kotwicki, De Robertis, von Szalay, & Towler, 2009; Montgomery & Hamilton, 1997; Stoner, 2004). For example, the μmoles photons m^2/s threshold at which shallow reef-dwelling king mackerel (*Scomberomerus cavalla*, Scombridae) cease foraging (Montgomery & Hamilton, 1997) is 557-fold higher than the threshold at which largemouth bass, a species that often dwells in freshwater lakes, ceases foraging (McMahon & Holanov, 1995). Lastly, light can be used as a fish attractant or repellent in the darkness (Freón & Misund, 1999), but this effect is species and wavelength specific (Marchesan, Spoto, Verginella, & Ferrero, 2005; see Sensory ecology section).

The influence of the moon on vulnerability may be more complex than simply acting as a waxing and waning light source. Exogenous rhythms, including the lunar cycle, are important cues for fish behaviour (Koukkari & Sothern, 2006; Takemura, Rahman, & Park, 2010) and there are many examples of fish following lunar cycles with respect to movement (Hernández-León, 2008) and reproductive behaviours (Danylchuk et al., 2011; Grabowski, McAdam, Thorsteinsson, & Marteinsdóttir, 2015; Takemura et al., 2010). Lunar effects have also been detected in freshwater (Horký, Slavík, Bartoš, Kolářová, & Randák, 2006), where there is little to no tidal effect, and in the deep sea (Wagner, Kemp, Matthheus, & Priede, 2007) where there is no light effect. For some species, the lunar phase is an important predictor of catch rates even after adjusting for increased fishing effort caused by preconceived beliefs that fishing is better during certain lunar phases (Cabanellas-Reboredo et al., 2014; Kuparinen et al., 2010; Poisson, Gaertner, Taquet, Durbec, & Bigelow, 2010; Vinson & Angradi, 2014). There are, however, also examples in which the effects of lunar cycles on vulnerability have been determined to be negligible or altogether non-existent (Lowry, Williams, & Metti, 2007; Ortega-Garcia, Ponce-Diaz, O'Hara, & Merilä, 2008).

Flow is a key driver of vulnerability because it alters how scents are distributed in the water (Atema, 1988) and it constrains the activity and movement of fish (Benito, Benejam, Zamora, & Garcia-Berthou, 2015). Both the position of a fish in the current relative to bait and the intensity of the current will affect the distance at which a fish can be attracted to bait (Løkkeborg & Bjordal, 1992; Løkkeborg et al., 2014). There are also costs to swimming in a current and some fish species are better adapted to holding/feeding in strong currents. Many fish species will shelter from or avoid strong currents or turbulent flows (Benito et al., 2015; Enders, Boisclair, & Roy, 2003; Herrala, Kroboth, Kuntz, & Schramm, 2014). This can increase encounters with hooks placed in refuge areas such as eddies in rivers, affecting the encounter (Figure 1). Catches of migrating Atlantic salmon (*Salmo salar*, Salmonidae) have also been linked to water flows (L'Abée-Lund and Aspås 1999; Crozier & Kennedy, 2001), possibly because it acts as a cue for upriver movement, which increases encounters with hooks.

Similar to flow, the wind can have a powerful effect on fish distributions and foraging behaviour. For example, wind speed may be a significant predictor of vulnerability in northern pike (Kuparinen et al., 2010). Wind creates turbulence and can influence upwell/downwell phenomena, which in turn may create altered distributions of temperature, prey or baits and their scents (Atema, 1988), stimulating hunger and an internally vulnerable state as well as generating unfavourable physical conditions for swimming (Lupandin, 2005; Roche et al., 2014). Additionally, wind-induced turbulence may reduce visibility via increased turbidity (Cózar, Gálvez, Hull, García, & Loiselle, 2005), which can alter the distribution of predators as a function of their sensory capabilities (Utne-Palm, 2002). In the strongest winds, fish have been observed to seek refuge (Munks, Harvey, & Saunders, 2015), altering encounters and vulnerability depending on the location of the refuge.

Some fish are sensitive to changes in hydrostatic pressure (Holbrook & de Perera, 2011; Ikegami et al., 2015; McCutcheon, 1966) and many intertidal marine fishes use changes in hydrostatic pressure as a zeitgeber for rhythmic behaviours adapted to the tidal cycle (Gibson, 1984). It is often suggested that fish can sense changes in barometric pressure and modify behaviour accordingly (Guy, Neumann, & Willis, 1992; Heupel, Simpfendorfer, & Hueter, 2003;

Jeffrey & Edds, 1999; Mallekh, Lagardere, Anras, & Lafaye, 1998). There is, however, a lack of consensus on this (e.g., Anras, 1995; Schulz & Berg, 1992) and the only direct test of barometric pressure changes on fish vulnerability found no relationship in northern pike (Kuparinen et al., 2010). Changes in barometric pressure are small and slow relative to the changes in hydrostatic pressure experienced by fish during even small vertical movements. For example, the pressure difference from swimming upward ~10 cm in the water column is equal to the change in barometric pressure from a typical high- to low-pressure system (Ikegami et al., 2015; Northcott, Gibson, & Morgan, 1991). Responses to barometric pressure are reactions to other weather changes or possibly to other weather changes correlated with changes in barometric in a predictable way (Cabanellas-Reboredo et al., 2014; e.g., infrasound).

The effects of the chemical abiotic environment are largely similar to those of the physical abiotic environment in that it alters the physiology and behaviour of the fish. A key component of the chemical environment is dissolved oxygen (DO), which limits the aerobic respiration of fish (Fry, 1971). Fish forage more and become more active when DO increases (Buentello, Gatlin, & Neill, 2000; Kramer, 1987) and they may be able to move into new foraging areas. The repercussions of these behavioural changes for fishing were measured by Weithman and Haas (1984), who found that every 1 mg/L reduction in DO under already hypoxic conditions reduced the catch rate of rainbow trout by 0.1 fish per angler hour. Environmental hypoxia may also constrain the distribution of fish in a system to alter the encounter with hooks (Prince & Goodyear, 2006).

3.2 | Biotic environment

The biotic environment is composed of living organisms (including predator and prey species) and creates contexts that contribute to the vigilance and vulnerability of fish (Figure 2). Many fish form groups or aggregations, which have dominance hierarchies (Hughes, 1992; Bumann and Krause 1993; Nakano, 1995). Within hierarchies, feeding may be structured so that dominant individuals have priority or higher quality territory where feeding is best (Vainikka, Koskimäki, Niemelä, & Kortet, 2012). Large fish have large territories (Grant & Kramer, 1990) and have access to more food such that they should be more vulnerable to capture (Tsuboi & Morita, 2004). Density-dependence in catches is relatively well developed (e.g., Shardlow, 1993) but factors such as competition, predation and social inhibition are concepts that are still emerging (Table S1).

Competition among conspecifics alters the internal state of fish and can increase vulnerability. Stålhammar, Linderfalk, Brönmark, Arlinghaus, and Nilsson (2012) found that releasing captured pike into groups of other pike reduced the latency to reinitiate feeding of the released individual, indicating that competition perceived from social context may initiate risk-taking activity and a faster transition back into the vulnerable state. Pfeiffenberger and Motta (2012) measured the suction feeding velocity of bluegill (*Lepomis macrochirus*, Centrarchidae) and found that it was influenced by social context, with competition for food inciting greater suction velocities. Information transfer among feeding fish is therefore clearly an important aspect of feeding and vulnerability although the interspecific differences have not yet been adequately described. Northern pike in experimental tanks exhibited social stress and reduced growth at high density, suggesting that catches would not necessarily be linearly related to density due to changes in internal state at high densities (Edeline et al., 2009). However, empirical work specifically in pike failed to find evidence for density-dependent catches by anglers (Pierce & Tomcko, 2003). Geographic features may further alter the vulnerability of fish; Mogensen, Post, and Sullivan (2013) described a latitudinal cline in catches of walleye (Sander vitreus, Percidae) and northern pike, with fish more vulnerable in northern lakes where the growing season is shorter and prey diversity is lower. This aligns with Raat (1991), who found zander (*Stizostedion lucioperca*, Percidae) catches to be highest in artificial ponds with low prey density, indicating that hunger and competition for food influenced the vulnerability of the stocks to fishing (see also Ware, 1972). Raat (1991) found, however, that the relationship between catchability and prey density changed seasonally, with fish in the autumn equally vulnerable regardless of prey density.

Social learning is a widespread mechanism in many fish species for acquiring information about both foraging and risk (Brown & Laland, 2003); it follows that social facilitation increases fish feeding in experimental settings (Ryer & Olla, 1991; Shardlow, 1993; Wright & Eastcott, 1982) and gregarious fish often rely on leaders to direct their movements towards food (Reebs, 2000). Fish are therefore more likely to feed in the presence of other feeding conspecifics and anglers take advantage of this effect by using groundbait to attract certain fishes, such as cyprinids (Arlinghaus & Mehner, 2003; Niesar, Arlinghaus, Rennert, & Mehner, 2004). Shardlow (1993) suggested that salmon are more vulnerable when in high densities due to social facilitation, but other authors (Mills, Mahon, & Piggins, 1986; Peterman & Steer, 1981) found that migrating salmonids tend to have lower vulnerability at high abundance. The probability of an individual in a group being captured also decreases with group size because the risk is spread out across a greater number of individuals. Naïve fish can learn to accept novel prey from observing experienced conspecifics (Brown & Laland, 2003) and therefore naïve fish should be capable of learning to avoid lures via observation; however, most research on social learning in foraging has focused on facilitation rather than inhibition (Table S1). Social scenarios could also create landscapes of fear in which the perceived risk of predation affects the behaviour and vulnerability of both captured and uncaptured fish (Alós, Puiggrós et al., 2015).

3.3 | Morphological traits

Fish species, populations and individuals differ in their physical morphology as a function of their life history, metabolism, habitat and nutrition. Fish do not randomly select resources for foraging and fishing success is related to the habitats frequented by fish and the food that they target (Bryan & Larkin, 1972; Sibbing, Osse, & Terlouw, 1986; Wimberger, 1994; e.g., Morita & Suzuki, 1999). Fishers often exhibit an understanding of how the fish morphology affects their catch by selecting gear (e.g., hook sizes) specific to the fishing context. In the

literature, body size is the best established morphological factor that contributes to vulnerability (Table S1) but we also address factors such as gape and shape and the emerging understanding of their role in fish vulnerability (Figure 2).

Fish size is perhaps the most important and well-developed trait that determines vulnerability (Table S1). Body size affects all three components of the vulnerability framework: internal state, encounter and gear selectivity (Figure 2). Juvenile fish often are not piscivorous and therefore many small fish would not strike most baits or lures (Miranda & Dorr, 2000). Large fish have a tendency to have greater food intake needs and higher resilience to changes in environmental factors such predation risk; they are less prone to predation than small individuals are and therefore often have increased activity. Higher food intake needs and dominance over small conspecifics can result in rank ordering of foraging that favours large individuals, making them more vulnerable to capture (Vainikka et al., 2012). Alternatively, large individuals may have access to higher quality territory or larger home ranges that makes them more likely to be encountered than other individuals (unless higher quality territory leads to greater encounter with natural prey and therefore less probability of noticing gear). Large individuals may have slower feeding rates because they consume larger food that take longer to process and therefore have longer food processing times (Miranda & Dorr, 2000). There is an important interface between the morphology of fish and the fishing gear (see Fishing gear section) in that the size selectivity of fish is related to the ratio of fish size and gear size (as in Mittelbach, 1981). Small fish may be invulnerable to large hooks as a consequence of the gape size (Arlinghaus et al., 2008; Erzini et al., 1997; Karpouzi & Stergiou, 2003; Millar, 1992). In most systems, the large fish tend to be more vulnerable to hooks but Tsuboi, Morita, Klefoth, Endou, and Arlinghaus (2016) demonstrated that fishing pressure could alter this relationship by increasing timidity of fish (Arlinghaus et al., 2016; Arlinghaus, Laskowski, et al., 2017).

Mouth morphology can also affect hooking success or hook placement (Cooke et al., 2003). Within species, mouth morphology can be relatively plastic and influenced by early life feeding experience, affecting the gear selectivity. Wintzer and Motta (2005) found that hatchery largemouth bass developed morphometric qualities associated with suction feeding, beneficial for feeding on pellets in the hatchery, rather than ram feeding (i.e., piscivory). Suction feeders do not chase prey as vigorously as ambush predators (Webb, 1984), with consequences for bait selection and retrieval method/speed of fishers.

Fish populations show large intraspecific variability in their body shape, which has been associated to different behavioural traits, such as swimming performance (Langerhans & Reznick, 2010; Jones, Palkovacs, & Post, 2013; Leris, Sfakianakis, & Kentouri, 2013), antipredator responses (Chivers, Zhao, & Ferrari, 2007; Domenici, Turesson, Brodersen, & Brönmark, 2008), habitat choices (Bourke, Magnan, & Rodríguez, 1997; Ehlinger, 1990) and adaptations to the local flow conditions (Franssen, Harris, Clark, Schaefer, & Stewart, 2013; Fulton, Bellwood, & Wainwright, 2005). Alós, Palmer, Linde-Medina, and Arlinghaus (2014) showed that fish with larger mouths and shallower, elongated bodies were most vulnerable to hooks. Individuals with larger mouth areas will be more prone to ingest hooks or lures than individuals with small mouths, but selection acted against shallower and more elongated bodies, suggesting an indirect selection for swimming behavioural traits that co-vary with morphology (Alós, Palmer, Linde-Medina et al., 2014).

3.4 | Life history

Populations from different parts of a species' geographic range may exhibit marked variations in life history traits such as breeding frequency, age at maturity, parity, or fecundity (Leggett & Carscadden, 1978; Mann, Mills, & Crisp, 1984). Life history traits such as growth rate, reproductive investment, and the age and size at maturation directly contribute to lifetime fitness and hence are under strong natural selection (Mousseau & Roff, 1987). The life history of an individual also contributes to vulnerability (Figure 2), and accordingly, a rich literature on the potential for fisheries to induce life history changes in an evolutionary sense has developed (reviews by Hard et al., 2008; Jørgensen et al., 2007; Kuparinen & Merilä, 2007). Recent works suggest the potential for fisheries to induce life history changes in an evolutionary context certainly exists even for species mainly exploited by hook and line recreational fisheries (Arlinghaus, Matsumura, & Dieckmann, 2009; Saura et al., 2010; Alós, Palmer, Catalan et al., 2014).

Some life history traits and specific life history strategies relate closely to fisheries vulnerability, such as decisions when and where to aggregate or spawn and how to trade-off risk of predation and energy acquisition-related behaviours that ultimately foster growth (Enberg et al., 2012), even in hook and line recreational fisheries (Alós, Palmer, Catalan et al., 2014). Species with predictable spawning migration patterns have increased encounter probability (see Movement section) with fishers at consistent times, and both Consuegra, Verspoor, Knox, and De Leániz (2005) and Pérez, Izquierdo, de la Hoz, and Garcia-Vazquez (2005) observed selection for maturing Atlantic salmon that entered freshwater earliest. Nest guarding species such as the North American black basses (*Micropterus* spp., Centrarchidae) are more vulnerable to fishing gear during the nest protection phase of their life history (Suski & Philipp 2004; Philipp et al., 2009; Sutter et al., 2012). Fishers can exploit spawning fish and cause significant declines in abundance without necessarily affecting catch rates as for example revealed for barred sand bass (*Paralabrax nebulifer*, Serranidae) and kelp bass (*Paralabrax clathratus*, Serranidae) stocks in southern California, USA (Erisman et al., 2011). Seasonally predictable aggregation behaviour in the life history of fishes fosters intense exploitation by fishers, leading to hyperstability in catch rates.

The relevance of life history traits for vulnerability can be understood in the context of underlying physiology, behaviour and traits that correlate with life history. Work by Klefoth (2017) and Alós et al. (2016) confirm these findings for recreationally targeted freshwater and marine species. Natural selection often favours large body size and high fecundity whereas artificial selection selects against large body size and high fecundity, altering the fitness landscape (Alós, Palmer, Catalan et al., 2014). For most species, larger individuals are

generally more vulnerable to angling (Askey, Parkinson, & Post, 2013; van Poorten & Post, 2005; Tsuboi & Endou, 2008). Therefore, fisheries can be size-selective (e.g., Miranda & Dorr, 2000). It is debatable whether fishes for which vulnerability is strongly behaviour-based have strong life history responses. Instead, one can predict fisheries-induced timidity without necessarily a response in growth (Arlinghaus, et al., 2016; Arlinghaus, Laskowski, et al., 2017).

3.5 | Cognitive ecology

Learning and forgetting complicate the temporal dynamics of vulnerability. These cognitive processes modify the propensity of a fish to strike lures and allow a fish to draw on experienced or observed capture events (Figure 2). Fish learning is a well-studied topic (reviewed in: Thorpe, 1963; Gleitman & Rozin, 1971; Kieffer & Colgan, 1992; Laland, Brown, & Krause, 2003). The capacity for learning varies widely among species (Coble, Farabee, & Anderson, 1989), life stages (Coble et al., 1989; Hawkin, Armstrong, & Magurran, 2008; Hutchison et al., 2012) and environments (biotic: Magurran, 1990; Huntingford & Wright, 1993; Brydges, Heathcote, & Braithwaite, 2008; abiotic: Girvan & Braithwaite, 1998; Girvan and Braithwaite 2000; Strand et al., 2010; Ferrari et al., 2012). Some research on learning and conditioning in the context of foraging can be interpreted in the context of vulnerability, but empirical research into this, and particularly in forgetting, is less common (Table S1). Nonetheless, the influence of fish cognition on vulnerability is wide-ranging.

In passive fishing (e.g., setline, bobber fishing), fish encounter baits while foraging, which is a process with a significant learning component (Warburton, 2003). Foraging performance is modified by experience through repeated exposures to prey items (Warburton & Thomson, 2006; Ware, 1971) and by associations of prey items with specific cues (Wisenden & Harter, 2001). For this reason, a fish will not become vulnerable to certain fishing gears until it learns to forage for the prey item that it imitates (i.e., gear selectivity; Figure 1). Consequently, individuals may differ in bait choice based on their experience. According to Shepard's law of generalizations (Shepard, 1987, 1988; Warburton, 2003), fish should respond more strongly to stimuli with pre-existing associations. In addition to explaining why fish learn to strike certain baits, this law also suggests that it will be increasingly challenging for a fish to avoid gear that mimics normal food items, particularly live bait (e.g., Beukema, 1970b).

The first indications that fish can learn to avoid capture were from observations of declining catch rates over time (Aldrich, 1939). Such declines in catch rates are commonplace in recreational fisheries (Anderson & LeRoy Heman, 1969; Beukema, 1970a,b; Raat, 1985; Young & Hayes, 2004; Klefoth et al., 2013; Alós, Palmer, et al., 2015; Alós, Puiggrós, et al., 2015; Colefax, Haywood, & Tibbetts, 2016), but it is challenging to establish a causal relationship between learning to avoid baits and these declines. Other factors that co-vary with catch rate declines over time, such as seasonal environmental changes, must first be ruled out as causes (van Poorten & Post, 2005). Askey, Richards, Post, and Parkinson (2006), however, found that an approximately three-fold decline in catch rates of rainbow trout after 15 days of fishing in experimental lakes was best explained by intrinsic individual differences in vulnerability combined with learned hook avoidance and not seasonal changes. Fernö and Huse (1983) and Klefoth et al. (2013) also observed rapid declines in catch rates over time in more controlled tank and pond environments where fewer variables could be confounding. Acquired gear avoidance may, however, be gear specific (Alós, Palmer et al., 2015), and Lennox, Diserud et al. (2016) found that significantly more recaptured Atlantic salmon were captured on a different gear from that of the initial capture, suggesting avoidance only of familiar gear.

Studies demonstrate that fish can avoid fishing gears after capture and evidence suggests a learning effect (Lennox, Diserud, et al., 2016) but the exact mechanisms are not completely clear. For instance, declines in catch rates could occur via a shift in the movement or space use of fish (Alós, Puiggrós et al., 2015; Cox & Walters, 2002; Matthias et al., 2014), altering encounter rates (Figure 1). Fish can be conditioned to gear avoidance as shown experimentally by Mackay (1977), in which gear avoidance was induced by intoxicating baits with lithium chloride. The proximate cues that fish associate with capture are not known and are not necessarily the gear itself. It is possible that fish learn to change their behaviour around cues only sometimes associated with fishing such as boat noise (Jacobsen et al., 2014).

Some fish show no decline in vulnerability over time (Tsuboi & Morita, 2004). For example, cutthroat trout (*Oncorhynchus clarkii*, Salmonidae) were captured on average 10 times in one season (once every 5 days; Schill, Griffith, & Gresswell, 1986). In that case, the fish never learned to avoid the gear, had a very short memory of the gear, or were desperate to forage. Certainly, learned information is rarely retained permanently, which is demonstrated by a wide range of forgetting times that have been recorded in fish (Brown, Ferrari, & Chivers, 2013; Coble et al., 1989). Novel predator recognition was forgotten after 21 days in rainbow trout (Brown & Smith, 1998) and novel predator cue recognition was forgotten after 2 months in fathead minnows, *Pimephales promelas* (Chivers & Smith, 1994). Longer memory retention has been found in crimson spotted rainbow fish, *Melanotaenia duboulayi*, which learned to avoid a trawl for up to 11 months (Brown, 2001) as well as in carp, which avoided recapture for up to 1 year (Beukema, 1970a). Like other animals, memory retention in fish is likely partly a function of the reinforcement schedule and the strength of the cognitive associations between stimuli and response. Forgetting may be an adaptation to cope with uncertainty in environments (Brown et al., 2013) and the memory retention of fish will be related to the eco-evolutionary history of a population. In more uncertain, rapidly changing environments, information should be less reliable over time (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005) and therefore the optimal memory retention time should be shorter (Fernö, Huse, Jakobsen, Kristiansen, & Nilsson, 2011; Ferrari, Brown, Bortolotti, & Chivers, 2010). Because the availability of reliable information should be measurable across environments, life history strategies and life stages (Brown et al., 2013; Ferrari et al., 2010), this concept could allow for better predictability of when and how long a fish will learn to avoid capture.

3.6 | Metabolic physiology

Metabolic rates vary among individual fish and can affect their behaviour and performance (Biro & Stamps, 2008; Careau & Garland, 2015; Careau, Thomas, Humphries, & Réale, 2008), which in turn contribute to vulnerability to fishing gear (Cooke, Suski, Ostrand, Wahl, & Philipp, 2007; Redpath, Cooke, Arlinghaus, Wahl, & Philipp, 2009 Redpath et al., 2010). High energy and oxygen demands often correlate with boldness, activity, exploration behaviour (Jenjan, Mesquita, Huntingford, & Adams, 2013) and learning (e.g., Mesquita, Borcato, & Huntingford, 2015; Sneddon, 2003; Tudorache, Blust, & De Boeck, 2007). These integrated phenotypes have a metabolic foundation (Careau et al., 2008) that contributes to the vulnerability phenotype (Uusi-Heikkilä et al., 2008; Table S1).

Variation in standard metabolic rate can affect the behavioural output and the life history productivity of individuals (Biro & Stamps, 2008) so that the metabolic rate and boldness-related expressions of the fish are often positively associated (Killen, Marras, Ryan, Domenici, & McKenzie, 2012). Activity and boldness are positively related to growth (Biro, Morton, Post, & Parkinson, 2004; Redpath et al., 2010). Consequently, selection (including artificial selection; Brauhn & Kincaid, 1982) can drive evolution of growth and metabolic rates in a direction that decreases vulnerability of fish. Domesticated fish often have fast growth and metabolism and are thus good models of highly vulnerable phenotypes (Klefoth et al., 2013).

Individuals with a fast standard metabolic rate increase their maximal metabolic rate to maintain energetic scope (Priede, 1985). Metabolic scope might impact vulnerability to fishing as it is known to influence aerobic activity (Priede, 1985), recovery after catch-and-release (Killen, Costa, Brown, & Gamperl, 2007) and foraging activity (Fu et al., 2009), which together impact foraging success and energy acquisition behaviours because increased oxygen demands impact energy acquisition and risk-taking (Biro et al., 2004). When comparing two strains of largemouth bass selected for their vulnerability to angling, Cooke et al. (2007) found resting cardiac activities (an indirect measure of metabolic rate) to be significantly elevated in highly vulnerable fish. Redpath et al. (2010) similarly found standard metabolic rate, maximal metabolic rate and metabolic scope to be significantly slower among largemouth bass with low angling vulnerability. These studies indicate high metabolic costs for fish that are vulnerable to fishing (Philipp et al., 2015) such that highly vulnerable fish should search for and consume more food (Cooke et al., 2007; Redpath et al., 2009). These differences in energetic demands affect foraging behaviour, energy conversion and feeding urgency (Nannini, Wahl, Philipp, & Cooke, 2011), ultimately influencing the internal state and encounter of fish with gear (Figure 2).

Transient physiological states of hunger influence vulnerability of fish in the short-term (Raat, 1991; Redpath et al., 2009, 2010). Among the factors that motivate fish to strike baits, including aggression, social facilitation and curiosity, hunger has the greatest influence on fish vulnerability by modifying the internal state (Bryan, 1974; Stoner, 2004). Hunger stimulates food search behaviour and reduces risk-avoidance behaviours such that it increases both encounters and the gear selectivity (Atema, 1980; Godin & Crossman, 1994; Heermann et al., 2013; Løkkeborg et al., 2014). Hunger is modulated by the neuroendocrine system (Fletcher, 1984), especially the peptide hormone ghrelin. Ghrelin is implicated in the release of growth hormone and in the regulation of food intake and hunger in mammals (Nakazato et al., 2000). Stimulation of feeding behaviour is likely to have a similar neuroendocrine foundation in fish, and ghrelin has been demonstrated to stimulate feeding in rainbow trout (*Oncorhynchus mykiss*, Salmonidae; Shepherd et al., 2007; but see Jönsson et al., 2007 for conflicting results) and goldfish (*Carassius auratus*, Cyprinidae; Unniappan et al., 2002; Unniappan, Canosa, & Peter, 2004). Although the exact hormonal mechanisms remain unclear in the vulnerability literature (Table S1), hunger is key to the internal state of the fish and is central to vulnerability of feeding fish. Whether this is also true among fish that are not actively feeding (e.g., migrating salmon) is not known. The response to baited hooks by fish has been shown to differ as a function of their recent food consumption (Løkkeborg, Olla, Pearson, & Davis, 1995; Stoner, 2003; Stoner & Sturm, 2004) and food-searching behaviour correspondingly increases with food deprivation (e.g., Løkkeborg et al., 1995; Stoner, 2003; Stoner & Sturm, 2004). These motivations to feed also influence hook ingestion, and food-deprived whiting (*Merlangius merlangus*) and cod (*Gadus morhua*) swallowed a hook more rapidly and were more often hooked in the stomach (Fernö, Solemdal, & Tilseth, 1986; Johannessen, 1983). It follows that fish that are satiated or near satiated become more selective of prey items whereas fish that are hungry are easier to capture, affecting individual vulnerability (Olla, Katz, & Studholme, 1970).

3.7 | Movement

The probability of capturing a fish depends on the spatial and temporal distribution of predator (fishers) and prey (fish), and thus the encounter probability between each other (Figure 2). Biological encounters are described in the fields of movement ecology and optimal search behaviour in predator-prey systems (Viswanathan, Raposo, & da Luz, 2008), both in animal (Humphries et al., 2010; Viswanathan, 2010) and human systems (Raichlen et al., 2014). An encounter event occurs given the coincidence of individual fish and fishing gear in time and space, allowing for the interaction of fish and fisher and creating the potential for the fish to be hooked. The final capture of the individual fish or overall vulnerability is ultimately a function of the probability that an individual will strike a hook, which depends on the internal state of fish and properties of fishing gear (Figure 2). The spatial dimensions of fishing encounters are small but vary greatly depending on the environment (e.g., turbidity; see section on Abiotic environment section). The temporal dimension of encounter is much more variable, ranging from seconds to hours, when a fish is moving around the gear but is difficult to hook. Encounters between fish and fishing gear will involve a diffusive aspect (stochastic searches) and a reactive component, similar to normal foraging in fish (Vermard, Rivot, Mahévas, Marchal, & Gascuel, 2010; Viswanathan et al., 2008; Walker et al., 2014). Better resolution of movement in the study of fish vulnerability is now possible with tracking technology, but presently

much of the research has focused on movement of fish rather than of the fishers (Table S1).

The encounter probability of a fish with fishing gear is analogous to a predator-prey system that can be modelled by measuring the movements of predator and prey (Alós et al., 2016). Some exceptions are scenarios in which fishers actively search for relatively stationary fish (e.g., when the largemouth bass is defending the nest; Cooke et al., 2007) or in which static bait depends exclusively on movement of the fish for encounter (e.g., fishing with bait suspended motionless in the water column by a float or bobber, Lennox, Whoriskey, Crossin, & Cooke, 2015). We focus on situations where fish and fishers are both mobile. The most widely applied movement models for describing fish movement are random walk (RW) processes (Horne, Garton, Krone, & Lewis, 2007; Turchin, 1999), which are implemented to describe the movements observed in different fishing scenarios and targeted species (Smouse et al., 2010). RWs can be applied for calculating the probability of encountering fishing gear (e.g., Martins et al., 2014; Patterson, Basson, Bravington, & Gunn, 2009; Viswanathan, 2010), and telemetry offers novel opportunities for understanding encounters and vulnerability (Baktoft et al., 2012; Cooke et al., 2004; Hussey et al., 2015). For example, a RW can delineate home ranges of fish (e.g., Alós et al., 2016; Palmer, Balle, March, Alós, & Linde, 2011; Pedersen & Weng, 2013) because fish frequently move predictably within a discrete home range area (Fagan et al., 2013; Kie et al., 2010). In addition, there is a relationship between swimming speed and gear encounter probability (Kallayil et al., 2003; Løkkeborg, Fernö, & Humborstad, 2010; Løkkeborg et al., 2014; Villegas-Ríos et al., 2014). Alós et al. (2016) and Alós, Palmer et al. (2012) showed exploration is a key movement trait of the home range behaviour determining the vulnerability of individual fish. How other general aspects of fish movement affect vulnerability, such as the size of the home range, depend on the fishery system and the stochastic component of the fish and fisher movement (Alós et al., 2016). There may be a relationship between home range size and vulnerability (e.g., in hunting systems; Ciuti et al., 2012). For example, Alós et al. (2016) found that small home range sizes of pearly razorfish (Xyrichtys novacula, Labridae) predicted low vulnerability to recreational fishing (but see Olsen, Heupel, Simpfendorfer, and Moland, 2012)

Experience and conventions of fishers dictate where fish are likely to be captured; as a result, individuals that go fishing more frequently are responsible for a higher proportion of the catch (Hilborn, 1985; Ortega-Garcia et al., 2008; Seekell, 2011; Seekell, Brosseau, Cine, Winchcombe, & Zinn, 2011). Limited information is available regarding how the fisher behaviour and movement influence encounter with the fish and the overall vulnerability (but see Hunt, 2005; Hunt, Arlinghaus, Lester, & Kushneriuk, 2011; Post & Parkinson, 2012; Cabanellas-Reboredo et al., 2014; Matthias et al., 2014), likely owing to difficulties collecting spatial data. In commercial fisheries, mandatory tracking devices (e.g., vessel monitoring systems; VMS) have improved the knowledge of the spatial distribution of fishing effort (Bertrand, Díaz, & Lengaigne, 2008; Gerritsen & Lordan, 2011; Mills, Townsend, Jennings, Eastwood, & Houghton, 2007; Walker et al., 2014). These systems have rarely been implemented in recreational fisheries where alterative observational surveys have been developed (Fraidenburg & Bargmann, 1982; Smallwood & Beckley, 2012). These require more personnel and equipment, and are especially difficult to apply in vast marine environments (Cabanellas-Reboredo et al., 2014). There is also a general lack of movement data of the search for fish, limiting our understanding of the role of movement of fishers into the vulnerability of fish (Alós et al., 2016). What is known is that boat fishers move following a two-state process characterized by a stop-and-go pattern where searching and fishing are combined during the fishing trip (Vermard et al., 2010). This stop-and-go has a stochastic component following a RW, but it is usually optimized to maximize encounters with fish and reduce cost (e.g., fuels) through super-diffusion processes that sometimes involve Lévy search patterns (Bertrand, Bertrand, Guevara-Carrasco, & Gerlotto, 2007; Bertrand, Díaz, & Ñiquen, 2004). Lévy walks offer an advantage for increasing encounter rates when the fisher moves rapidly relative to the fish and when the fish density is low (Bartumeus et al., 2002). Not all fishers are equally mobile in a landscape (Matthias et al., 2014); the extent of movement therefore has an important role determining the vulnerability of a given fish. According to Alós, Palmer et al. (2012), complex search patterns increase vulnerability by increasing encounters with fish, exerting a strong effect on the catchability of fish within a given stock. There is, however, a need for more empirical data (fisher trajectories and spatial data) to disentangle the role of the search pattern in the encounters with fish.

Movements of both fish and fisher follow some kind of optimization, decreasing the scale of the RW or reducing the stochastic component of both movement patterns, which can alter the encounter probability. Cognition and sensory systems are key determinants of the movement trajectories of fish (Nathan et al., 2008). Interactions between the fish and the fishing gear prior to a physical encounter can actually modify the movement pattern of fish, reducing or enhancing the probability of encounter. Bait or chum (i.e., ground baiting, prebaiting; Cryer & Edwards, 1987; Arlinghaus & Mehner, 2003; Niesar et al., 2004) can generate a chemical cue that attracts some fish, enhancing the probability of encounter (Løkkeborg, Bjordal, & Fernö, 1989). Recent research on carp, however, showed that encounters were insufficient to control vulnerability to capture, suggesting that fine-scale behaviour towards baited hooks ultimately drove the catch process (Monk & Arlinghaus, 2017; see Foraging ecology section). Movement of the gear also increases encounters (e.g., trolling; Meals, Dunn, & Miranda, 2012). The interaction between fish and fishing gear can, however, induce a landscape of fear, which notably can reduce the movement pattern of fish that witness other fish being captured or experiencing their own catch-and-release event (Januchowski-Hartley, Graham, Feary, Morove, & Cinner, 2011; Alós, Puiggrós et al., 2015; see Biotic environment section). Fish can reduce their encounters for example by swimming less or using refuges more, which modifies their natural movement patterns in response to the fisheries exploitation following this landscape of fear (Alós, Palmer et al., 2015). Thus, how the fished environment or how the fear of predation by fishers modulates movement patterns are important components of vulnerability by constraining encounter rates between fish and fishers.

3.8 | Sensory ecology

Fishes detect their immediate environment with sensory receptors tuned to solutes, gasses, temperature, bulk flow, electrical and magnetic fields, as well as light, acoustic vibrations, and textures (Horodysky, Cooke, & Brill, 2015) according to species-specific life histories and tasks (e.g., Horodysky, Brill, Crawford, Seagroves, & Johnson, 2013; Horodysky et al., 2010; Kajiura, Cornett, & Yopak, 2010; Kalinoski, Hirons, Horodysky, & Brill, 2014; Ladich, Collin, Moller, & Kapoor, 2006). Sensory information is received via the peripheral nervous system from visual, olfactory, gustatory, auditory, mechanoreceptive, and in some cases, electro- and magnetoreceptive channels (Hara & Zielinski, 2007); these multimodal sensory inputs are integrated via the central nervous system. Chemical and acoustic signals propagate the farthest from the stimulus source, followed by visual, mechanoreceptive, and lastly electrical information at progressively shorter ranges (Jordan et al., 2013). Successful detection of a stimulus by the relevant sensory channel requires contrast discrimination of a signal of sufficient intensity from its background (i.e., signal to noise; Nilsson, Warrant, & Johnsen, 2014). Signal detection does not guarantee capture success; fishes may be indifferent to, attracted by, or repulsed from the stimulus generated by the gear. There is considerable superstition among fishers in assessing how the sensory ecology of fish contributes to their vulnerability, but there are emerging applied studies (Table S1) as well as considerable fundamental science on the sensory mechanisms of vulnerability.

Many of the world's premier gamefishes forage visually and the gears that target them come in every imaginable shape, size, and colour combination (Clarke, 2006; Kageyama, 1999; Schultz, 1999). Most fishes of recreational importance possess duplex retinas and use rod photoreceptors during scotopic (dim/dark) conditions and anywhere from one to four types of cone cell photopigments under photopic (bright) conditions to extend visual performance (Crescitelli, 1991; Lythgoe, 1979). There are four principal properties of vision that affect fish vulnerability to fishing gear: luminous sensitivity (i.e., response to light intensity), chromatic sensitivity (response to wavelength), temporal resolution (speed of vision), and spatial resolution (acuity; Horodysky, 2009). Diel foragers have moderate sensitivity to dim light, with fast, highly acute visual systems attuned to a broader range of wavelengths (Horodysky, Brill, Fine, Musick, & Latour, 2008; Horodysky, Brill, Warrant, Musick, & Latour, 2008; Horodysky et al., 2010). Visual foraging requires sufficient light intensity for image formation; however, crepuscular foraging success can be enhanced via circling search behaviours that exploit the disruptive effects of rapid changes in solar azimuth angle and light intensity on prey camouflage strategies at dawn/dusk (Johnsen, 2003; Johnsen & Sosik, 2003). Visual cues to foraging may be addressed by fishers via selection of appropriate bait and lure sizes, shapes, colours (including contrast combinations), prismatic or flash-generating materials, and speed of retrieve (including bait/lure action) under the given optical conditions (Figure 2). Attachment of light sticks to illuminate baits may improve catches, as demonstrated for surface longlines with chemical light sticks that increased swordfish (*Xiphias gladius*) catches in a study by Hazin, Hazin, Travassos, and Erzini (2005). Although ultraviolet colours and glues are marketed as visual aids to hooks, many important gamefishes are insensitive to ultraviolet light and it is not likely to be relevant to vulnerability in most circumstances (A. Horodysky, unpublished).

Chemical signals linger in water and can disperse great distances from their source (Jordan et al., 2013). Fishes detect chemical stimuli through at least two different chemoreceptive channels: olfaction (smell) and gustation (i.e., taste; Hara, 1986; Vabø et al., 2004). Chemical stimuli may be categorized as attractive (including stimulants and enhancers that evoke food consumption) or distractive (including suppressant and deterrent compounds that evoke food avoidance or rejection; Kasumyan & Døving, 2003). Chemical solutions used to attract fishes typically include natural prey substances, including salts, sugars, as well as bile and amino acids (Carr, Netherton, Gleeson, & Derby, 1996), but may also include other natural (garlic, cheese) and anthropogenic (soaps, lubricants) substances (Hara, 1986, 2006a, 2006b; Kasumyan & Døving, 2003). Generally, L-alpha-amino acids are highly potent stimulatory compounds for many fishes (Caprio, 1984; Hara, Carolsfield, & Kitamura, 1999; Yamashita, Yamada, & Hara, 2006), even triggering innate bite responses in ictalurids and salmonids (Caprio et al., 1993; Valentinčič & Caprio, 1997). Salmonids and elasmobranchs also demonstrate strong olfactory responses to human skin and sweat odours, including a variety of amino acids, salts, and B vitamin compounds (Tester, 1963; Valdes, Olivares, Ponce, & Schmachtenberg, 2015). Fish gustatory systems and their peripheral organs (i.e., taste buds) may be expressed orally within the oral cavity, pharynx, oesophagus, and gills, or extra-orally along lips, barbels, fins, and body flanks (Kasumyan & Døving, 2003). Olfactory and gustatory responses to chemical signals differ among species; they may also vary within a species as a consequence of ontogeny, sex, strain, geographic region, and/or chemical exposure history (Hara et al., 1999). Many natural and artificial baits and lures are infused with olfactory and/or gustatory stimulants to increase encounters and gear selection by fish (see Foraging ecology section); however, there has been little empirical research (Table S1).

Fishers also target fish auditory (sound) and mechanoreceptive (vibration) systems to stimulate encounters and gear selectivity. Fishes receive auditory signals via vibrational differences between their otoliths and sensory epithelia (Fay & Popper, 1975); information from low-frequency vibrations and water flow is transduced by mechanoreceptive lateral line canals and free neuromasts (Bleckmann & Zelick, 1993; Montgomery, Coombs, & Halstead, 1995). Sound signals received by the fish auditory system consist of pressure and particle displacements that attenuate at different rates with distance from the source (Popper & Fay, 1999). Low-frequency auditory and mechanoreceptive stimuli can be of great importance in turbid waters or in vegetated habitats; for fishes such as red drum (*Sciaenops ocellatus*, Sciaenidae), mechanoreception is critical to foraging success (Liao & Chang, 2003). Many popular recreational fishing lures (i.e., spinnerbaits, spoons, crankbaits, and top water lures) displace water and create low-frequency stimuli as they are retrieved in order to improve gamefish attraction distance, albeit without scientific evidence in the literature (Table S1). Others include embedded rattles that may serve

a similar purpose, although fundamental frequencies of lure rattles are often beyond the auditory range of many gamefishes (A. Horodysky, unpublished). Low-frequency fishing-related noises (anchors, chains, hatch doors, etc.) are, however, within the auditory ranges of gamefishes and can radiate long distances under water, an auditory stimulus that can move fish from vulnerable to invulnerable (Figures 1 and 2). Alternatively, some offshore fishers believe that properly tuned boat propellers produce frequencies that are attractive to billfishes (Istiophoridae) and tunas (Scombridae; A. Horodysky, pers. obs).

Electroreceptive and magnetoreceptive channels of sensory information have received comparatively less attention from fisheries, because these abilities were lost in the evolution of most advanced bony fishes that are targeted by fisheries (Jordan et al., 2013). The ampullary electrosensory system of primitive fishes and elasmobranchs consists of pores and gel-filled canals that are highly sensitive at short-distances to low-frequency electrical stimuli produced by biotic and abiotic sources (Jordan et al., 2013; Kajiura et al., 2010; Kalmijn, 1971). Records of shark depredation of electronic biologgers suggest electroreceptive attraction (Kerstetter, Polovina, & Graves, 2004) and Porsmoguer, Bănaru, Boudouresque, Dekeyser, and Almarcha (2015) found that magnets on hooks increased catch rates of blue shark (*Prionace glauca*; Carcharhinidae). Other recent research demonstrates deterrent effects of electropositive metals, magnets, and semiochemical repellents on by-catch of sharks and sturgeon, although results are temperature- and species-specific and may be superceded by social cues when fishes aggregate (Bouyoucos, Bushnell, & Brill, 2014; Brill et al., 2009; Hutchinson et al., 2012; O'Connell, Stroud, & He, 2012; Robbins, Peddemors, & Kennelly, 2011).

3.9 | Foraging ecology

Integration of sensory cues is necessary for foraging, which ultimately renders most fish vulnerable to fishing (Jones, 1992). The foraging system of fish contributes to their vulnerability, particularly through species-specific differences in the preferred sensory mechanisms. Although the foraging ecology of a fish is essential to capture, it is difficult to empirically study and there are few studies of foraging systems and vulnerability of fish (Table S1). A considerable literature on foraging systems has the potential to provide relevant information on how foraging links to vulnerability (Figure 2).

The first phase of foraging is appetitive (Atema, 1980) and encompasses detection of and search for food. Appetitive foraging primarily integrates olfactory, auditory and seismosensory clues that indicate availability of food (Pavlov & Kasumyan, 1990; see Sensory ecology section). Although the gustatory and olfactory sensory systems of fish are fundamentally similar in that they are responsible for detecting waterborne chemicals, they are functionally different and serve distinct purposes for fish (Yamashita et al., 2006). Both gustatory and olfactory stimuli can be responsible for initiating food search activity (Valentinčič & Caprio, 1994, 1997); however, Hara (2006a,b) suggested that gustatory cues only play a complementary role in food search. Olfactory cues are therefore powerful signals for fish actively searching for food, and because they are dispersed almost entirely by the flow of water, fish down-current from the source detect them best (Løkkeborg, 1998). Chemotaxis, or orientation relative to chemical sensory cues, allows fish to seek food after it is perceived; Johnsen and Teeter (1985) found that bonnethead sharks (*Sphyrna tiburo*; Sphyrnidae) could detect differences in chemical concentrations between the right and left side and are therefore capable of using olfactory cues for orientation towards food sources.

Various mechanisms of chromatic sensitivity exist across fish taxa; genes coding for vertebrate opsin proteins evolved in jawless fishes and proliferate throughout the jawed fishes (Collin et al., 2003; Van-Eyk, Siebeck, Champ, Marshall, & Hart, 2011; Kalb, Schneider, Sprenger, & Michiels, 2015). Clear aquatic environments primarily reflect blue-green light (Kalb et al., 2015) but wavelengths of light attenuate with depth depending on the optical properties of water (including phytoplankton, organic and inorganic particulates, and products of vegetative decay; Lythgoe, 1975). Contrast is somewhat important for fish feeding, and predatory fish may increase the contrast of lit areas via concealment in shade (Helfman, 1981) or modify their behaviour to maximize prey detection and self-concealment (Huveneers et al., 2015). The perception of contrast in water is altered by many factors and the ability to use that information in feeding is difficult to establish. The movements of prey render them more visible to the eye (Meals et al., 2012; Utne-Palm, 2000) and can be perceived by the lateral line seismosensory system, which detects waves created by the movement (Kasumyan, 2003); for example, banded killifish (*Fundulus notatus*, Cyprinodontiformes) detect insects on the surface of water by sensing the vibrations made by the insect's wake (Schwartz & Hasler, 1966). Pohlmann, Atema, and Breithaupt (2004), moreover, determined that European catfish (*Silurus glanis*, Siluriformes) sensed the wake formed by prey movement, facilitating capture and New, Fewkes, and Khan (2001) found that American muskellunge (*Esox masquinongy*, Esocidae) integrate these seismosensory stimuli with visual information when detecting prey, reinforcing that the foraging ecology and vulnerability of fish is highly integrated and complex.

Once food has been detected or found, fish make movements to consume it. In the consummatory phase of feeding, visual assessment is important prior to strike but taste and texture are ultimate factors for fish prior to ingestion. Depending on the species and its foraging ecology, different strategies for identifying and appraising chemical cues in the water have evolved. Benthic feeding catfishes have highly concentrated external taste buds, particularly on the barbels, that are used to assess food quality. Catfish (*Ictalurus natalis*, Siluriformes) can consequently distinguish between food pellets and synthetic pellets—unless the synthetic pellets were scented by contact with natural pellets or by human hands (Atema, 1971). When synthetic pellets smelled like hands, the fish would ingest the pellet into the buccal cavity but reject the item during oral manipulation, suggesting that internal taste buds are better for distinguishing food than external taste buds. Largemouth bass have internal taste buds on the pharyngeal jaws that appraise the quality or suitability of potential food items prior to swallowing (Linser, Carr, Cate, Derby, & Netherton, 1998) and common carp have a muscular cushion in the mouth that allows post-feeding selection (Sibbing et al., 1986). Texture is also an important

component of manipulation and fish may reject food items with attractive chemical properties when the texture, plasticity or hardness is unappealing (Kasumyan, 2012).

3.10 | Fishing gear

The fishing gear is the final determinant of the fate of a given fish while it is internally vulnerable and has already encountered the fisher based on the selectivity of the gear (Figures 1 and 2). As in any other predator-prey system, the size of prey (i.e., the bait) that predators (i.e., the target fish) can capture and consume is directly related to predator length and gape size. Hook and bait size therefore influence the gear selectivity, the overall vulnerability, and a key outcome measure, catch per unit effort CPUE (Wilde et al., 2003; Alós, Cerdà, Deudero, & Grau, 2008; Arlinghaus et al., 2008; Figure 1). The fishing gear is therefore an important component of the vulnerability landscape (Alós, Palmer, Linde-Medina et al., 2014; Cerdà et al., 2010). Large individuals are generally more vulnerable because of ontogenetic dietary changes and increased physical interactions between the hook and the fish generating size-related gear selectivity (Carbines, 1999; Miranda & Dorr, 2000; Cooke, Barthel, Suski, Siepker, & Philipp, 2005; Grixti, Conron, & Jones, 2007; Rapp, Cooke, & Arlinghaus, 2007; Alós, Palmer, Grau, & Deudero, 2008; Alós, Cerdà, et al., 2008; Tsuboi et al., 2016; Boulêtreau et al., 2016). The differences are likely to be species-specific, but gear size is ultimately an important component of vulnerability because the probability of catching a fish is a function of the ratio between the size of the gear and the size of the fish (Erzini et al., 1997; see Morphological traits section). This topic is one of the best studied in terms of vulnerability, particularly in relation to hook shapes and sizes and their effects on fish catch (Table S1).

Some empirical evidence suggests that not only the size of the hook or bait, but also the type of fishing gear may affect vulnerability of a given fish. Natural bait type affects CPUE in hook and line commercial fisheries (Broadhurst & Hazin, 2001; Løkkeborg & Bjordal, 1992; Woll, Boje, Holst, & Gundersen, 2001). Smith (2002) detected a relationship between the type of natural bait (either maggots or chironomids) and the vulnerability of the fish. Aydin (2011) compared sardine (*Sardina pilchardus*, Clupeidae) and onyx (*Solen vagina*, Solenidae) in a Turkish recreational fishery and found that onyx captured considerably more fish than sardine; however, individuals with higher condition factors were more frequently captured using sardine. Similarly, Alós, Arlinghaus et al. (2009) found that the Mediterranean fishes were more vulnerable to worms than to shrimp, suggesting that the proper selection of bait by the fisher can move fish from an invulnerable to a vulnerable state.

Fish are often more vulnerable to natural baits than to the artificial ones (Arlinghaus et al., 2008; Payer, Pierce, & Pereira, 1989), and there is a relationship between the vulnerability of fish and the type of artificial bait (Orsi et al., 1993; Wilson et al., 2015). For example, many specialized recreational anglers believe that soft plastic baits are more effective than spoons or crankbaits, and some scientific work corroborates this (Danner, Chacko, & Brautigam, 2009; Arlinghaus, Alós, et al., 2017). Some authors have suggested that the colour of the artificial lure can move fish to the vulnerable state (see Sensory ecology, Foraging ecology sections; Hsieh et al., 2001; Moraga, Wilson, & Cooke, 2015). Colour is surely context-dependent, for instance, surface lures are simply silhouettes on sunny days (this extends to many other contexts as well). A variety of tools are marketed for supplementing gear but are poorly studied, including chemical light sticks, scents, or rattles. Schisler and Bergersen (1996) conducted one assessment of artificial scents on bait and found that scented baits had more instances of deep hooking than unscented baits or artificial flies, suggesting a difference in the selectivity of the two gears. Dunmall, Cooke, Schreer, and McKinley (2001), however, identified no such relationship, indicating that the hooking injuries were more likely related to fishing style with the scented baits. Depending on the target species, hook size, hook number, hook shape, or bait type (i.e., natural or artificial) could be regulated to moderate the capture of non-target species or the capture of undersized or oversized individuals. As an example, Alós, Arlinghaus et al. (2009) found that shrimp captured fewer undersized fish and reduced the frequency of deep hooking, suggesting that regulating the bait type used by fishers could be an effective means of controlling the catch. One aspect traditionally overlooked by the scientific community (but with high attention in the fishing community) is how the natural bait is presented or how the artificial lure moves to simulate natural prey (e.g., speed of retrieval of crankbaits, drift speed of dry flies).

Finally, the different management regimes adopted in the fishery influence vulnerability per se. Fisheries management strategies can move fish from vulnerable to invulnerable through the stipulation of technical measures and input and output regulations. Input controls (i.e., regulation of effort) such as restrictions on the number of licenses or restrictions on the size of vessels and/or gear are also stipulated in fisheries. Input regulations reduce the fishing effort, altering the probability of encounters between fish and fishers and thereby vulnerability. Camp, van Poorten, and Walters (2015) demonstrated how a seasonal closure may move fish to vulnerable states to maximize fishers' satisfaction. Alternatively, output regulations directly regulate the catch, which can be taken from the fishery and may move fish to invulnerable states when fishers reach maximum allowable quotas or catches. Cerdà et al. (2010) demonstrated that increasing the minimum allowable hook size shifted the vulnerability landscape in the fishery away from small fish, a measure that could be implemented to conserve small sized individuals and could be applied to many different fisheries given appropriate data. Similarly, length-based harvest regulations affect which sizes are vulnerable to harvest (Gwinn et al., 2015; Lennox, Falkegård, Vøllestad, Cooke, & Thorstad, 2016). The policy scenario determined by the different management regimes therefore is a consideration in the vulnerability of fish to hooks.

4 | CONCLUSIONS AND RESEARCH NEEDS

Vulnerability to hooks depends on interrelated factors but the key components can be broken down to internal state dynamics, encounters, and physical aspects of the fishing gear. By drawing attention to the mechanisms driving these three components, our work provides a

common framework between traditionally isolated disciplines such as fisheries science, ecophysiology, or movement ecology that facilitates understanding the drivers of the fate of fish in fisheries. By establishing a complex vulnerability framework, we provide a mechanistic explanation for trait-selective fisheries that should facilitate the study of the causes and consequences of fisheries-induced evolution of exploited fish in hook and line fisheries. The challenge is now to provide data in each specific fishery to determine what the main drivers of vulnerability are. Certainly, the determination of the main drivers would require a shift toward interdisciplinarity, as our complex vulnerability framework suggests (Figure 1).

The encounter component of vulnerability is probably the most difficult and least developed concept at present, owing to a paucity of data (Table S1). Encounters between fish and fishers provide the spatial and temporal axes of vulnerability. Understanding the emergent movement properties of fish and fishers can notably enhance our understanding of why a fish is captured. With the recent development of biotelemetry (Hussey et al., 2015; Krause et al., 2013) and biologging (Cooke et al., 2016), we can measure movement and other traits (e.g., physiology using accelerometers or heart rate loggers) that can contribute to vulnerability as well as develop an understanding of how correlated traits and environmental factors generate a vulnerability landscape (Figure 1). Advances can be made in relating fish vulnerability and movement using experimental lakes, bays or reefs with tagged fish and passive telemetry arrays and may even be enhanced by incorporating trait data of fish released with tags (e.g., metabolism, personality, morphology) or by using biologgers to characterize acceleration, depth or temperature use of fish (Cooke et al., 2016). These tools enable behavioural assessments in the wild. Understanding the spatial component of fishing effort is already contributing to improved management in some commercial fisheries (Booth, 2000; Lorenzen et al., 2010; Post & Parkinson, 2012). Most of the management decisions in fisheries are based on population dynamics models that incorporate fishing effort but typically assume that both effort and fish abundance are spatially homogeneous (Lynch, 2006). Incorporating encounter rates as one aspect of vulnerability and population catchability should provide a better understanding of the population dynamics of exploited stocks and further development of sustainable fisheries.

Our review (Figure 2) of fisheries vulnerability synthesizes what we know about the factors contributing to vulnerability and mortality of fish. However, our review of the factors puts how much remains unknown about factors driving fish vulnerability to capture into perspective. We established that many factors are important, but we cannot yet determine how important they are, particularly relative to one another, and without proper appreciation of contextual differences. Also, we found that some areas have seen more study than others (Table S1). For example, salmonids have received considerable attention relative to other species, likely owing to their popularity in commercial, subsistence, and recreational fisheries. The components of vulnerability as we outline them above have been shown to contribute to fish feeding behaviour, success or capture and (sometimes by extension) to fisheries vulnerability. Some components are certainly more important contributors to vulnerability than others. We do know, however, that some factors, such as hunger, increase the probability of a fish being vulnerable and physiological hunger is probably relatively important to vulnerability compared to other factors, and we also know that encounter is a necessary yet often insufficient condition for capture (Monk & Arlinghaus, 2017). Fish catchability is described by coefficients or probabilities of capture as a population-scale metric (Arreguín-Sánchez, 1996), but the same cannot be said for vulnerability: a fish is either vulnerable or invulnerable to fishing. Whereas an invulnerable fish will never be captured by fishing gear, by definition a vulnerable fish will always be captured by fishing gear because the state of the fish is otherwise unobservable.

Ultimately, a more comprehensive understanding and appreciation of fish vulnerability (with appropriate application) has the power to contribute favourably to satisfying both management and fisher objectives. Understanding vulnerability is of critical importance considering that the individual heterogeneity in many fish traits are correlated with vulnerability (i.e., some fish are bolder than others; Conrad et al., 2011). Underappreciating the influence of vulnerability can induce incorrect conclusions at population scales and consequently affect fisheries management. According to foraging arena theory (Ahrens et al., 2012), moreover, fish cluster into vulnerable and invulnerable pools in wild stocks. Interactions with humans produce changes in the fraction of fish in the vulnerable and invulnerable states (Alós, Palmer et al., 2015). The importance of accounting for dynamics in individual vulnerability to predation is well documented in ecosystem models such as Ecopath with Ecosim (Walters & Martell, 2004). The mechanistic approach to vulnerability provides the tools for understanding not only the number of fish in the vulnerable state, but also what the mechanisms are that move fish between vulnerable and invulnerable states (exchange rates), contributing to an estimate of catchability at the population scale. Large vulnerable pools of fishes (i.e., high catchability) produce larger benefits to society in terms of food provisioning in commercial fisheries and angler satisfaction in recreational fisheries (Arlinghaus et al., 2014). Understanding the major drivers of exchange has the potential to produce many benefits to fisheries science and the sustainable exploitation of aquatic resources (Ahrens et al., 2012). The path forward to understanding vulnerability requires interdisciplinary work because many different fields of biology, physics and chemistry interact to determine the vulnerability of an individual fish (Figure 2).

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