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On the relevance of animal behavior to the management and conservation of fishes and fisheries

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Abstract There are many syntheses on the role of animal behavior in understanding and mitigating conservation threats for wildlife. That body of work has inspired the development of a new discipline called conservation behavior. Yet, the majority of those synthetic papers focus on non-fish taxa such as birds and mammals. Many fish populations are subject to intensive exploitation and management and for decades researchers have used concepts and knowledge from animal behavior to support management and conservation actions. Dr. David L. G. Noakes is an influential ethologist who did much foundational work related to illustrating how behavior was relevant to the management and conservation of wild fish. We pay tribute to the late Dr. Noakes by summarizing the relevance of animal behavior to fisheries management and conservation. To do so, we first consider what behavior has revealed about how fish respond to

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key threats such as habitat alteration and loss, invasive species, climate change, pollution, and exploitation. We then consider how behavior has informed the application of common management interventions such as protected areas and spatial planning, stock enhancement, and restoration of habitat and connectivity. Our synthesis focuses on the totality of the field but includes reflections on the specific contributions of Dr. Noakes. Themes emerging from his approach include the value of fundamental research, management-scale experiments, and bridging behavior, physiology, and ecology. Animal behavior plays a key role in understanding and mitigating threats to wild fish populations and will become more important with the increasing pressures facing aquatic ecosystems. Fortunately, the toolbox for studying behavior is expanding, with technological and analytical advances revolutionizing our understanding of wild fish and generating new knowledge for fisheries managers and conservation practitioners.

Keywords Ethology · Fish behavior · David Noakes · Conservation behavior

Introduction

The study of animal behavior (including both ethology and behavioral ecology) has a long history, but it was not until Konrad Lorenz, Niko Tinbergen, and Karl von Frisch were awarded the 1973 Nobel Prize in Physiology and Medicine for their research on individual and social behavior patterns that animal behavior was widely embraced as a formal discipline (Moreno and Muñoz-Delgado 2007; Goodenough et al. 2009). Notably, Tinbergen's famous four questions, which serve as categories of explanation for animal behaviors (Tinbergen 1963), have withstood the test of time and still represent the dominant paradigm in animal behavior scholarship (Bateson and Laland 2013; Burkhardt 2014). The field has further developed with effort focused on understanding the fundamentals and foundations of animal behavior (Houck and Drickhamer 1996) and an emphasis on animal-environment interactions (i.e., behavioral ecology; Owens 2006). Yet, animal behavior also has applications in quantifying and enhancing animal welfare (Mench 1998), increasing production in agri/aquaculture (Baxter 1983), training of companion animals (Horwitz 2008), and for informing the conservation and management of wildlife (Sutherland 1998). The latter application — conservation and management of wildlife — has developed into its own discipline known as conservation behavior (Blumstein and Fernández-Juricic 2004) (Fig. 1).

Conservation behavior was formally acknowledged as a discipline beginning in the 1990s and early 2000s with the publication of several conceptual papers (Sutherland 1998; Buchholz 2007; Caro and Sherman 2011; Caro 2016) and books (Caro 1998; Blumstein and Fernández-Juricic 2004; Berger-Tal and Saltz 2016) that illustrated the benefits of animal behavior research for addressing conservation and management problems. This acknowledgement was followed by articles that took a more pessimistic view towards the interface of behavior and conservation (see Caro 2007; Angeloni et al. 2008), as well as the publication of a conceptual framework (Berger-Tal et al. 2011). Today, many examples demonstrate how animal behavior has helped us understand how humans affect wildlife (Tuomainen and Candolin 2011; Wong and Candolin 2015) and how animal behavior is increasingly used to improve conservation and management interventions (Blumstein 2015). However, existing syntheses on conservation behavior contain few examples with fishes, while examples with birds, mammals, herpetofauna, and even invertebrates are featured prominently. We regard this lack of focus on fishes to be a simple oversight given the taxonomic foci of most of the authors of conservation behavior synthesis papers.

Fishes are the most speciose group of vertebrates (Helfman et al. 2009). They can be found from high elevation freshwater lakes to the abyss of ocean basins and from the Amazon River to under the Antarctic Ice Shelf. Global marine and freshwater fish populations face a number of threats. Indeed, there is

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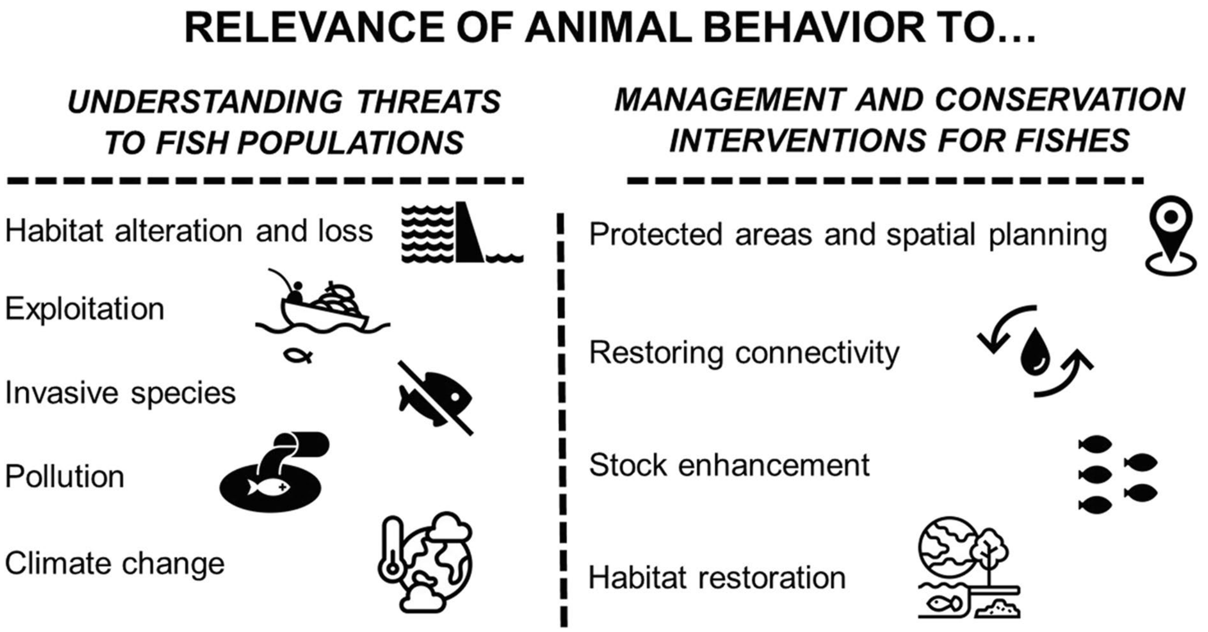

Fig. 1 Graphical depiction of the ways in which animal behavior is relevant to understanding threats to fish populations and informing the conservation and management of fishes

ample evidence documenting widespread population declines linked to various threats (Arthington et al. 2016; Gordon et al. 2018; Reid et al. 2019) and the identification and mitigation of key threats is urgently needed so that fish populations can be conserved or restored. Moreover, for fish populations that are doing well, there is a need to ensure that management actions are effective. Fish provide numerous ecosystem services including some with direct benefit to humans by supporting nutritional security (Islam and Berkes 2016), and livelihoods and cultures (Holmlund and Hammer 1999; Lynch et al. 2016), which provide compelling examples of why fish populations need to be managed sustainably. Underpinning the contemporary science-based management and conservation of fishes is an evidence base that brings together stock assessment data and knowledge of fish biology, physiology, genetics, and behavior.

Many researchers who study the behavior of fishes do so with the goal of generating knowledge that can be used by decision makers to achieve conservation and management objectives. Over the years, there have been a few highly focused reviews, such as applications of behavior in freshwater fisheries (O'Hara 1986), in stock assessment (Fréon et al. 1993), or on applications of acoustic telemetry tracking data to management (Crossin et al. 2017). The only synthesis on the relevance of animal behavior to fisheries and fish conservation (i.e., Shumway 1999) was published two decades ago in Environmental Biology of Fishes as part of a special issue on behavior and fish conservation (see Volume 55, Issue 1–2; Helfman 1999). This topic was of great interest to the late Dr. David L. G. Noakes — the long serving Editor of Environmental Biology of Fishes, as well as our friend, colleague, and mentor. Dr. Noakes was an influential behaviorist (see Muir 2022) who did foundational work illustrating how behavior was relevant to the management and conservation of wild fishes. Here, we pay tribute to Dr. Noakes by summarizing the relevance of animal behavior to fisheries management and conservation, with a focus on key threats to fishes, as well as common management interventions. This synthesis focuses on the totality of the field, but we also include a section where we summarize some of the unique contributions of Dr. Noakes and reflect on some of the themes that emerged from his work. Our synthesis spans freshwater and marine systems and is intended to be a resource for those with an interest in the application of behavioral tools, concepts, and knowledge to managing and conserving wild fish populations.

On the functional links between behavior, fitness and populations

To contextualize why those responsible with managing and conserving fishes should be concerned with fish behavior, we first provide a brief summary of the functional links between behavior and fitness with links to population-level processes. Behavior is fundamental to the organism-environment relationship (Owens 2006) whereby the environment can both constrain or stimulate behaviors, often operating through physiological mechanisms (e.g., energetics, locomotion, endocrinology; Ricklefs and Wikelski 2002). The behavior of individuals can affect their fitness (i.e., survivorship and lifetime reproductive success; Sutherland 1996). For example, activities such as foraging, social interactions and antipredator behavior are involved in the demographic performance of individuals via their influence on growth, condition, and reproductive rate/output (Sumpter and Broomhead 2001). Individual behavioral decisions (e.g., if and when to migrate, which habitats to occupy, when to forage vs seek refuge) can influence population parameters such as recruitment, population abundance, age at maturity, number of reproductively active adults, and mortality rates, among others (McNamara and Houston 1986). Conservation practitioners and resource managers tend to be primarily concerned with population-level processes (e.g., are they increasing, decreasing, stable), yet it is individual-level behavior (and physiology) that directly connects animals (including fishes) to their environment (Cooke et al. 2014; Horodysky et al. 2015; Bailey et al. 2022) and at times, their vulnerability to harvest/exploitation (e.g., Horodysky et al. 2015; Sbragaglia et al. 2022). As such, it is through the environment that stressors are often applied and realized on behavior and fitness (Killen et al. 2013). Behavior can vary greatly among individuals in the same population with individuals and groups responding differently to natural and anthropogenic threats and management actions (Goss-Custard and Sutherland 1997, Villegas-Ríos et al. 2022) and thus, contributing to variation in fitness across multiple scales (Smith and Blumstein 2008).

Relevance of animal behavior to understanding threats to fish populations

Habitat alteration and loss

Fishes have evolved a rich diversity of behaviors that allow them to exploit the environment and habitats around them to ultimately maximize their fitness. Whether a fish requires thousands of kilometers of riverine habitat, or a single cave within a coral reef, intact habitats and corridors among habitat patches are critical to sustain fish behaviors and life histories. In recent decades, habitat alteration and loss have intensified within aquatic ecosystems, particularly the degradation of lotic systems to support various human uses (e.g., energy production, flood control, irrigation, agriculture, sand mining; Tickner et al. 2020). As habitat is altered or lost, the fitness benefits associated with that habitat are altered, changing the way that fish behave in those environments. Indeed, fish behavior is dynamic and substantial plasticity in behavioral responses to environmental change is evident (Pitcher 1992).

Understanding of the behavioral ecology of fishes, and the interactions between fishes and their environments, can provide important insights into the effects of habitat loss and alteration on fish species (Scherer 1992). Many tools exist to study the behavior of fish in altered and fragmented landscapes (e.g., telemetry, mark-recapture, direct/video observation; Hussey et al. 2015). Regardless of the tool employed, the premise is that changes in fish behavior resulting from habitat change are a useful indicator of the influence of those impacts on the individual fish. As such, it is critical that the behavior of fish is compared to that of fish unimpacted by habitat alteration. As an example, in South America, migratory fish in dammed river reaches are generally unable to move upstream beyond dams, and they also tend to avoid the slow, lentic habitat associated with the reservoirs upstream of dams (Pelicice et al. 2015). Similarly, low-head barrier dams that were installed or maintained to limit migrating adult invasive sea lamprey (*Petromyzon marinus*) from accessing spawning habitat in rivers flowing into the Laurentian Great Lakes also restrict the upstream movement and reduce the biodiversity of desirable (non-target) species (see Table 1; Porto et al. 1999; Dodd et al. 2003; McLaughlin et al. 2006). In Lake Erie, one of the Great Lakes,

Table 1 David Noakes' contributions to the behavior, management, and conservation of fishes

Category	Sub-category	Findings	References
Threats	*Habitat alteration and loss*	Fish biomass and production is lower in channelized than in natural stream sections	Portt et al. 1986
		Brook Trout (*Salvelinus fontinalis*) are less reactive to disturbance in habitats with abundant habitat structure	Grant and Noakes 1987
		Young Brook Trout seek out velocity refuges to save on swimming costs without affecting foraging rate	McLaughlin and Noakes 1998
		Spawning areas for Brook Trout were positively associated with areas of groundwater discharge, which protected redds from ice	Curry and Noakes 1995; Curry et al. 1995
		Short-term variability in discharge caused by hydroelectricity peaking regimes could have negative effects on natural groundwater supply around Brook Charr redds	Curry et al. 1994
	Invasive species	Low head barrier dams used to restrict the upstream movements of sea lamprey in streams have negative effects on the movement and biodiversity of non-target species	Porto et al. 1999; Dodd et al. 2003; McLaughlin et al. 2006
		Non-native male Chinook Salmon (*Oncorhynchus tshawytscha*) interfere with the reproduction of Atlantic Salmon impeding re-introduction efforts in Lake Ontario	Scott et al. 2003; Scott et al. 2005c
		Non-native juvenile Chinook Salmon and Brown Trout (*Salmo trutta*) negatively affect the behavior of re-introduced Atlantic Salmon	Scott et al. 2005b
		Non-native Atlantic Salmon are able to navigate using the geomagnetic field, perhaps facilitating their invasion of novel habitats	Scanlan et al. 2018
	Pollution	Brook Trout alevins avoid low pH and elevated concentrations of aluminum, facilitating survival in acidifying waters	Gunn and Noakes 1986
		Pulse exposure to acidic Aluminum-rich water has negative effects on the fitness of Lake Trout embryos	Gunn and Noakes 1987

Table 1 (continued)

Category	Sub-category	Findings	References
Management interventions	*Protected areas and spatial planning*	Territorial behavior limits population density and potentially regulates population abundance of stream-dwelling Salmonids	Cole and Noakes 1980; McNicol and Noakes 1981; McNicol and Noakes 1984; Grant et al. 1989
		Aggressiveness, mobility and trophic specialization are inherited traits of juvenile Charrs, which facilitates adaptation to diverse habitats and ecological speciation	Ferguson and Noakes 1982; Ferguson and Noakes 1993
		Magnetic maps are inherited traits of Salmonids, facilitating their migratory life history patterns	Putman et al. 2014b
	Restoring connectivity	Removal of barriers promotes the movement of stream fishes and increases upstream species richness	Porto et al. 1999; Dodd et al. 2003
		Glass eels use two forms of locomotor behavior, active swimming and vertical climbing which facilitate their swimming into rivers and then over barriers	Linton et al. 2007
	Habitat restoration	Rainbow Trout held in high-density conditions suffered from higher levels of physiological stress than those at lower densities	Noakes and Leatherland 1977
		Reproductive behavior of captive-bred Atlantic Salmon is sufficiently natural to expect some success of restoration programs	Scott et al. 2005a
		Salmonids imprint on their natal magnetic fields, so rearing Salmonids in locations with unnatural fields may hinder attempts to stock or reintroduce populations	Putman et al. 2013; Putman et al. 2014a
		Exposing Salmon embryos to the olfactory signature of sites for future stocking may improve reintroduction success	Scanlan et al. 2018
		The success of restoration programs for Charrs will depend on the strengths of competition and predation in target fish community	Noakes and Curry 1995

hypoxic bottom layers caused by agricultural nutrient input displaced benthic fishes, changing the vertical distribution of prey fishes to the benefit of walleye (*Sander vitreus*), a key fishery target species (Brandt et al. 2011). Behavioral changes such as these are a clear indication of the impacts that habitat loss and alteration can have on fish fitness, and for species with specific niches or habitat requirements, large-scale habitat alterations can result in a complete loss of lifetime fitness (e.g., Pacific salmon *Oncorhynchus* spp.; Groot and Margolis 1991). With the staggering amount of fish movement and habitat use data generated by fish telemetry tracking, it seems likely that in the near future we will see many powerful examples of how those data can be used to quantify the effects of habitat change and loss on the behavior of fishes.

Exploitation

Somewhat ironically, exploitation (and overfishing) of fish stocks has been, in part, supported by our ever-growing understanding of the behavior of fishes (including traditional and Indigenous ecological knowledge), with early fishing settlements forming around accessible areas where fish aggregate in high abundance (e.g., kelp forest, coral reefs; Steneck and Pauly 2019), along migration routes, or at spawning sites (Sahrhage and Lundbeck 2012). Through the industrialization of fishing, the spatial extent and magnitude of exploitation has increased, leading to regional extirpation and ultimately the collapse of some fisheries. Indeed, exploitation is the most important threat to at-risk marine fishes in Dr. Noakes' home country of Canada (Woo-Durand et al. 2020). While information is less certain for inland systems and smaller fisheries (Deines et al. 2017; Hilborn et al. 2020; Ovando et al. 2021), exploitation ranks as the 4th most important major threat to freshwater fishes in Canada (Woo-Durand et al. 2020) and Dr. Noakes' adopted country of the USA (Wilcove et al. 1998). While the diversity of fishes and fish behavior was a driving force behind the range of capture methods that have been developed (Wardle 1986), the more formal study of fish behavior in the context of improving fisheries and fishing technology did not arise until the 1950s (Fréon and Misund 1999). This quickly expanded, however, to also develop more effective stock assessment and habitat or population protections to reduce exploitation and work within more tractable catch limits.

In addition to exploitation reducing the size and persistence of a fish stock, it may also alter the life history or behavior of the fishes that remain within the population by preferentially selecting for behavioral phenotypes that reduce catchability, which can lead to fisheries-induced evolution (Kuparinen and Merila 2007; Uusi-Heikkilä et al. 2008). For example, passive fishing approaches (e.g., gill nets, trapping, angling) preferentially catch bold, aggressive, or more active individuals, while more active gear (e.g., trawling, seining) captures shy or social individuals (Biro and Post 2008; Arlinghaus et al. 2017; Monk et al. 2021). In the former case, bias in capture can result in exploitation-induced timidity syndrome, whereby individuals that remain in a population may struggle to maintain social groupings, fail to reach their spawning grounds, or exhibit overall reductions in their dispersal and movement (Arlinghaus et al. 2017). Given the documented correlation between some behaviors (e.g., boldness or aggressiveness) and life history parameters (e.g., size at maturity or growth; reviewed in Biro and Stamps 2008), selection for specific behaviors within populations may result in lower yield, smaller stock sizes, or reduced catchability (Jørgensen et al. 2007; Arlinghaus et al. 2017; Guerra et al. 2020). Alternatively, behavioral diversity can provide resilience to a stock, such as Pearly Razorfish (*Xyrichtys novacula*) in Mallorca; Alos et al. (2015) found that daytime chronotypes of the Razorfish were most vulnerable to fishing but this phenotype was not heritable, so nighttime chronotype fish could evade capture and replenish the population, a behavioral buffer to overexploitation.

Considering protection of diverse behavior and life history phenotypes (see Shumway 1999) remains a conceptual and pragmatic challenge for fisheries managers. Management options may include temporal or spatial restrictions on fishing or adjustments in the type of fishing gear, but regardless of the method, the approach should aim to protect the portfolio of observed variation in behavior of the targeted species (Olsen et al. 2012). Sound management practices can support the recovery of overexploited stocks and prevention of exploitation of stocks that are currently stable (Hilborn et al. 2020), and a species' behavioral ecology will be essential in informing the development of such practices. Animal behavior (often alongside sensory physiology; Elmer et al. 2021) can also be exploited to develop bycatch mitigation strategies such as those that reduce bycatch by identifying how to spatio-temporally focus fishing efforts on target species (O'Keefe et al. 2014) or that involve study of gear types to identify opportunities for avoiding bycatch (Parsons et al. 2012; Martin and Crawford 2015).

Invasive species

Behavior plays an essential role in mediating species invasions, including the traits of species that determine their invasiveness, as well as those of native organisms that enable species invasions (Holway and

Suarez 1999; Weis and Sol 2016) and developing and implementing control or eradication methods (e.g., Bravener and McLaughlin 2013). Species invasions are also a dynamic multi-stage process where behavioral interactions change, often resulting in alterations to the behavioral tendencies of both native and invasive species (Ruland and Jeschke 2020). Synthesizing the role of behavior in species invasions, Sol and Weis (2019) concluded that invaders generally exhibit high levels of behavioral plasticity that facilitate their success in novel environments and that behavior is linked with many traits that affect invasiveness, including life history traits. Invaders often experience high resource availability and low predation pressure, which may contribute to more bold, aggressive, and highly dispersive behavioral phenotypes relative to native counterparts or even invaders in longer established areas (Myles-Gonzalez et al. 2015). However, this is not always the case based on a study of pumpkinseed in their native and introduced range where native fish were more bold (Ashenden et al. 2017). Bold, aggressive behavioral characteristics can also help invaders to outcompete native species that occupy a similar niche and drive invasion expansion through intraspecific competition (Hudina et al. 2014). For example, Noakes and colleagues suggested that inter-specific competition from non-native brown trout *Salmo trutta* and Pacific salmon were impeding the attempts to restore Atlantic salmon *Salmo salar* to Lake Ontario (Scott et al. 2003, 2005b, c; Table 1). Predator release often occurs due to behavioral factors, where native predators are present with the physical capacity to prey on the invader, but the predators fail to adapt to a new prey source because they do not recognize it as prey or lack the hunting tactics to effectively prey upon them (Sih et al. 2010). Similarly, prey species can also fail to detect, recognize and avoid novel invasive predators and experience high predation rates.

In the context of management, knowledge of species traits, including behavior, can help identify high-risk invaders and proactive steps to reduce the potential for their introduction and spread (Kolar and Lodge 2001). In cases where invasive species have become established, the behavioral responses of predators and prey often determine the longer-term role of the invader and changes to community structure in non-native ecosystems. For example, Round Goby (*Neogobius melanostomus*) have become hyper-abundant in established areas of the Great Lakes basin of North America. Further, Round Goby have become important prey for many predators, such as Smallmouth Bass (*Micropterus dolomieu*), resulting in increased growth rates and abundance (Steinhart et al. 2004; Morissette et al. 2018). Efforts may also be undertaken to help to condition native predators to effectively prey upon novel invasive species, such as culling invasive Lionfish (*Pterois* spp.) by helping sharks and groupers learn that lionfish are potential prey (Diller et al. 2014). However, in most instances, behavioral conditioning is unlikely to be a stand-alone solution to controlling or mitigating an established invasive species and its impacts.

Understanding the invasion potential of species to reduce their introduction is the only known and highly effective means of combatting the negative effects of introduced species. Indeed, once established, invasive species are nearly impossible to eradicate and expensive to control. For example, low-head barriers have been critical to the control of invasive Sea Lamprey in the Laurentian Great Lakes, North America. The barriers reduce the amount of tributary spawning habitat that Sea Lamprey can access and the amount of larval rearing habitat that is treated with chemical lampricides (Hrodey et al. 2021). However, as Noakes and his students have shown, these barriers also restrict the movement of native fishes (Porto et al. 1999), impact habitat (Dodd et al. 2003), and affect the distribution and abundances of native species (McLaughlin et al. 2006; see Table 1). Thus, our need to control invasions must also be balanced with our need to conserve native species. Once established, species invasions are dynamic and the behavioral characteristics of both invaders and native species change through time, which can have cascading effects on ecosystem structure and vulnerability to subsequent invasions (Ehrenfeld 2010). Knowledge of the behavior of invasive fishes derived from telemetry studies (reviewed in Lennox et al. 2016) is increasingly revealing opportunities for control by identifying areas of aggregation where control measures can be applied (e.g., identifying tributary use of Grass Carp [*Ctenopharyngodon idella*] in Lake Erie to guide the deployment of nets and electrofishing used to catch and remove the carp; Harris et al. 2021).

Pollution

A variety of pollutants (e.g., acidity, metals, pesticides, pharmaceuticals) can have detrimental consequences for aquatic species and ecosystems (Gunn and Noakes 1986, 1987; Saaristo et al. 2018). Measurements of physiology and fitness are commonly used when assessing the effects of aquatic pollution (e.g., Gunn and Noakes 1987). In contrast, the measurement of behavioral change associated with pollutants has garnered less attention (Jacquin et al. 2020), despite its proposed use in ecotoxicology dating back over 50 years (Warner et al. 1966) and the recent emergency of behavioral ecotoxicology (Ford et al. 2021). The earliest suggestions of why behavioral indicators have the capacity to be used as indices of sub-lethal toxicity still stand true (Dell'Omo 2002): they are an integrated result of many biochemical and physiological responses, tend to be sensitive, and can be obtained non-invasively (Warner et al. 1966). Avoidance responses of brook trout alevins in redds were crucial to their ability to survive pulses of low-pH conditions (Gunn and Noakes 1987; Table 1). Beyond avoidance responses, pollutants can alter much more complex forms of behavior. Acidification, herbicides, and thermal effluent can interfere with fish reproduction by influencing nest-building activity, courtship, offspring defence, and parental care (Jones and Reynolds 1997). More recently, attention has also been placed on the behavioral effects of non-chemical pollutants such as light and noise. For example, light pollution was shown to increase overall activity levels and disrupt the circadian rhythm of activity in nesting Smallmouth Bass, with potential consequences for energy use during a highly demanding life history stage (Foster et al. 2016). Pollution can similarly interfere with group behaviors. Groups of juvenile Seabass (*Dicentrarchus labrax*) exposed to playbacks of marine pile-driving are less able to coordinate their movements, showing less correlated directional and speed-related changes, cohesiveness, and directional ordering (Herbert-Read et al. 2017). Reproductive ecology could also be affected in organisms such a Burbot (*Lota lota*) which use drumming muscles on their swim bladder to generate noises coincident with their under-ice spawning (Cott et al. 2014). This intimate communication could be compromised by ice-road noise in northern regions (Cott et al. 2012).

Collectively, mounting evidence shows that behavioral responses to pollutants form an important link in understanding how pollutants influence individual fitness, population persistence, and ecosystem health, and therefore, the level of threat a pollutant poses (Jacquin et al. 2020). As links between sublethal behavioral effects and fitness are established, there will be potential to incorporate behavioral assays as more formal components of overall threat assessment and decision-making for fish populations in relation to a broad suite of pollution types (Jones and Reynolds 1997). By understanding how responses may change with varying levels of pollution, behavior also permits researchers and managers to predict the outcomes of pollution episodes and prioritize mitigation efforts (Jacquin et al. 2020). Understanding how pollutants impact avoidance and exploration behavior also has applications for determining how larger-scale processes in wild populations, such as migration or habitat selection, may be affected by increasing pollution levels (Malik et al. 2020).

While the application of behavior to the management of fishes facing pollution is gaining more traction, a number of research areas are ripe for further attention. First, much of the information we have about the influence of pollution on fish populations comes from studies investigating a single pollutant at a time. However, many individuals can be impacted by multiple types of pollution simultaneously, requiring studies that take a multi-stressor approach (McCarthy et al. 2008; Jacquin et al. 2020). Second, measuring multiple behavioral traits to gain more complete information on how fishes are responding to different forms of pollution can be a valuable approach. For example, marine noise pollution can affect swimming, shoaling, exploration, predator avoidance, nest attendance, territoriality, and sheltering behaviors, but rarely has more than one behavior been measured in the same study (Di Franco et al. 2020). Lastly, we still lack understanding on the level of inter-population variability in behavioral responses to pollutants (Jacquin et al. 2020). For instance, in the Laurentian Great Lakes, cleanup of many heavily polluted areas of concern (AOCs) has resulted in recolonization by fishes such as Lake Sturgeon (*Acipenser fulvescens*) and Lake Whitefish (*Coregonus clupeaformis*). While the exact mechanism is unknown, enhanced water quality is hypothesized to be a factor (Manny et al. 2015). However, this variation is highly relevant to determining how susceptible different populations may be to specific pollutants, and therefore how to best predict changes and manage them.

Climate change

Behavioral variation in fishes complicates our ability to project how they will respond to global climate warming, especially for species that live in thermally heterogeneous environments. Behavioral thermoregulation has long been studied in fishes (Keenleyside and Hoar 1954; Ferguson 1958; Magnuson et al. 1979) and some species clearly are adept at using temperature variability to their advantage. For example, Dogfish (*Scyliorhinus canicula*) make diel vertical migrations along a north-temperate sea mount to rest in deeper, cooler waters at night — a behavior that was conclusively motivated by a bioenergetic benefit rather than being caused by prey availability or predation risk (Sims et al. 2006). Bonefish (*Albula vulpes*), a species of the coastal tropics, shifted their foraging behavior to avoid what was otherwise a preferred nearshore foraging habitat when nearshore water temperatures reached upper extremes (Brownscombe et al. 2017). Temperate freshwater fishes experience dynamic temperatures. For example, habitat use by Lake Trout (*Salvelinus namaycush*) shifts seasonally as the thermal profile of lakes change, with concomitant changes in energy transfer and effects on prey fish communities (Guzzo et al. 2017). Knowledge about how fishes thermoregulate in the field can be useful for bioenergetic modeling to project future variability in growth and reproductive output. In Lake Erie, water temperature appears to at least partially drive an annual basin-wide migration of Walleye (*Sander vitreus*; Kershner et al. 1999, Raby et al. 2018). Knowing the temperature thresholds that cause fish to migrate or shift habitats could be useful from a fisheries planning standpoint, because fish movement can affect fisheries prosecution, assessment, and management (Sims et al. 2004; Crossin et al. 2017). It might be possible to use data now widely being generated with electronic tags (e.g., biologging and biotelemetry) to develop spatially and temporally explicit bioenergetic models that consider within and among individual variation in body temperature (Brownscombe et al. 2017), as long as appropriate bioenergetic calibrations are available for the species and sensor types being deployed.

The terrestrial ecology literature is replete with examples of how climate warming can cause phenological mismatches, whereby behaviors (e.g., migration) are either set based on photoperiod, and therefore, inflexible to changes in temperature, or triggered by temperature in ways that can be maladaptive when temperature regimes change dramatically (Robinson et al. 2009). In fishes, there are fewer examples, but the same types of behavioral problems can occur in response to a changing climate. Sockeye Salmon (*Oncorhynchus nerka*) have a relatively fixed schedule for their spawning migration. With the aid of geomagnetic imprinting (Putman et al. 2013; Table 1), migration begins hundreds or thousands of kilometers from river entry and ends in streams and rivers that drain into lakes upstream of the marine environment (Farrell et al. 2008). The relative inflexibility in timing of these migrations has up to now, appeared to be a problem, particularly for fish migrating upstream in summer that are encountering warmer temperatures, sometimes causing high en route mortality (Martins et al. 2011). Even if summer-run stocks were to shift their migration timing to late summer or early fall when temperatures are cooler, that would reduce among-stock diversity in spawn timing which in turn makes fisheries management more difficult (Schindler et al. 2010). Unlike Salmon, Sims et al. (2004) found that the timing of Flounder (*Platichthys flesus*) migration is sensitive to thermal variation, with profound implications for fisheries planning.

Apart from movement and migration, the thermal choices of fish in the laboratory can be used to predict their ecologically optimal temperature range in the wild. A variety of behavioral arena designs have been used to do so over the years (Christensen et al. 2021). In most cases, laboratory experiments are the only way to assess the ‘true’ thermal preferences of fishes (because other influences like food and predators can be controlled in the lab), but thermal preference behavioral tests have not proliferated widely (e.g., unlike the use of CTmax, or respirometry, to assess thermal performance), perhaps because the experiments are time-consuming and technically challenging (Speers-Roesch and Norin 2016). Animal-borne electronic tags with temperature sensors, in thermally mapped environments, can in some cases provide clear signals about what temperatures fishes prefer or avoid (Peat et al. 2016). Extensive mapping of thermal macro- and micro-habitat can be challenging, especially at biologically meaningful scales where secondary inputs and seeps can provide thermal refuge at difficult-to-measure scales. Nevertheless, effective examples exist, such as in a Canadian lake that became isothermal and reached supra-optimal temperature for Lake Trout. Here, telemetry-tracked Lake Trout congregated in the cold water plume from a groundwater discharge site that provided thermal refuge (Snucins and Gunn 1995). In Atlantic Salmon parr, conspecific chemical cues appear to help fish locate thermal refuge during severe heat waves (Elvidge et al. 2017). Spawning Brook Trout prefer to spawn in areas of groundwater discharge, which protect redds from the increasing variation in temperature that will accompany climate change (Curry and Noakes 1995; Curry et al. 1995; Table 1). Ultimately, understanding a given species' behavioral preferences and tendencies around temperature is useful for mapping available habitat and projecting future changes, both of which can be useful for conservation planning and mitigation.

Relevance of animal behavior to management and conservation interventions for fish

Protected areas and spatial planning

Spatial management of fisheries has historically been an essential component of the management toolbox (Hyrenbach et al. 2000; Suski and Cooke 2007), which necessarily draws on fish ethology. Unlike terrestrial systems where ecotones and species distributions are relatively well-defined, underwater spatial management poses a greater challenge (Lennox et al. 2019). The aquatic realm is dynamic with currents, fronts, eddies, and clines that can form invisible boundaries for fish or alternatively be exploited to save energy and move, thereby maximizing bioenergetic efficiency. Animal behavior has advanced rapidly with the increasing availability of electronic tags to remotely observe fish underwater, which has allowed us to estimate the paths of individual fish and estimate their space use. Resulting locational data contribute to estimating migration timing, range size, and residency time in certain areas as well as fidelity to specific habitats, resource selection, fishing and predation vulnerability, and landscape energetics (Hussey et al. 2015). These metrics are essential for testing the robustness of boundaries drawn for spatial management (noting that political and socio-economic factors also tend to be determinants for planning), which can include protected areas as well as zoning limits for aquatic infrastructure (e.g., fish farms, tidal energy, shipping) that limit disturbance to critical species and habitats.

With movement metrics, spatial management measures can be evaluated and refined. For example, areas that are too small to protect fish from fishing can be revealed by tracking behavior of individuals. Tracking may occur before implementation of spatial management in order to draw effective boundaries or after delineation to evaluate performance. Tracking animals within a protected area can provide data to evaluate their home range, core area use, or network dimensions based on relocations of the individual (e.g., Filous et al. 2017). Poorly situated protected areas can be revealed by matching detections to habitat types and assessing resource or step selection from a random subset of alternative habitats in the area (Griffin et al. 2021). If critical habitats are not included in a protected area, fish will not be well protected and spatial management will fail (e.g., Martin et al. 2020). Lea et al. (2016) specifically showed that marine protected area boundaries needed to expand in the Seychelles to properly cover shark habitat use. In the future, spatial management of fish resources may become more dynamic based on knowledge of fish presence and absence, as well as other species such as sea turtles (*Cheloniidae* spp.) that may be vulnerable to bycatch. Telemetry will continue to play a key role in ascertaining where and when fish move including testing performance of protected areas and other spatial management schemes. However, visual (e.g., baited underwater video; Whitmarsh et al. 2017) or auditory monitoring of fish with hydrophones (Luczkovich et al. 2008) may soon become more common non-invasive tools for tracking individual movement via spatial-capture-recapture to track presence and absence of fish and estimate space use within and beyond protected areas.

Restoring connectivity

Loss of habitat connectivity is one of the most pervasive threats to fish movement (Dudgeon et al. 2006;

Reid et al. 2019). Restoring and improving connectivity is thus one of the biggest challenges for fisheries conservation and management. For connectivity enhancement to be meaningful and effective however, it should be informed by knowledge of fish behavior. For example, knowing the distance of upriver migration can provide information for prioritizing barrier removal, or where fish passes may be constructed to be most effective (Branco et al. 2014). Noakes and colleagues illustrated this point in a study of the upstream migration of glass eels in Iceland (Table 1). At water temperatures above 4.5 °C, glass eels exhibited swimming behavior, which facilitated their entry into rivers during the early summer (Linton et al. 2007). However, climbing behavior only occurs at the warmer temperatures encountered in streams, which allows the eels to bypass natural barriers and proceed further upstream (Linton et al. 2007). Information on the timing and phenology of migration (and other movements) can help managers refine hydropower operations to improve passage during peak migration (Aarestrup et al. 2018; Birnie-Gauvin et al. 2019). While great effort is devoted to enhancing connectivity for migratory species, connectivity is also necessary for species generally viewed as non-migratory (Brevé et al. 2014; Benitez et al. 2018). Many fishes still move within freshwaters as they feed, reproduce, or seek refuge. Identifying where and when these various events occur can help managers decide where and when connectivity is most needed. Behavior can also be used to evaluate the effectiveness of connectivity enhancement projects (e.g., fishways, barrier removal) by evaluating differences in behavior before and after connectivity measures have been implemented.

Various approaches can be used to explore the behavior of fishes within the context of connectivity, with telemetry being one of the most common approaches used (Hussey et al. 2015). For example, acoustic telemetry showed that threatened Silver Perch (*Bidyanus bidyanus*) in the Murray River, south-eastern Australia occupied large areas that extended over hundreds of kilometers and over multiple habitat types, demonstrating that connectivity across these habitat types was important to prevent further population declines of this imperiled species (Koster et al. 2021). In another study, environmental DNA (eDNA) was used to monitor spawning migrations of Danube Bleak (*Alburnus mento*) and Vimba Bream (*Vimba vimba*). Specifically, daily counts were highly correlated to eDNA signals when flow was accounted for, providing managers with a non-invasive method to study fish behavior (Thalinger et al. 2019). Regardless of the method used, a greater understanding of fish behavior is necessary to focus efforts aimed at restoring connectivity for greatest benefit to fishes.

Habitat restoration

Habitat refers to the three-dimensional spatial units in which organisms reside that contain the physical, chemical, and biological attributes (Brind'Amour and Boisclair 2006) that facilitate survival and reproduction of individuals in a population. Habitat requirements differ across species and can vary over time in response to ontogenetic changes in the behavior and physiology of organisms, seasonal changes in habitat availability or suitability, and ecosystem instability. With aquatic ecosystems across the globe suffering from extensive habitat loss and degradation (Dudgeon et al. 2006; Arthington et al. 2016), ecological restoration has the potential to protect biodiversity (Bernhardt et al. 2005). Indeed, the United Nations has declared 2021–2030 the "Decade on Ecosystem Restoration," which aims to improve habitat and combat climate change (UNEA 2019). Underpinning efforts with a holistic understanding of behavior across all phases of restoration (i.e., planning, executing, and monitoring; see Hobbs and Norton 1996) is fundamental to maximizing restoration effectiveness (Caro 2007).

Habitat restoration can occur on a variety of spatial scales. For example, in aquatic ecosystems, habitat restoration has included interventions like liming of acidified lakes (e.g., Nyberg 1984; Booth et al. 1986), control and removal of invasive species (e.g., Frazer et al. 2012; Siefkes et al. 2013), dam removal (e.g., Catalano et al. 2007), and construction of artificial spawning reefs (e.g., Clark and Edwards 1999; Marsden et al. 2016). Regardless of spatial scale, the goal of habitat restoration intervention is to establish and conserve self-sustaining populations of target organisms, but often this goal is not met. Hale et al. (2020) proposed a framework highlighting how knowledge of animal behavior can be used to improve habitat restoration, centering on two critical questions that should be considered prior to, during, and after undertaking a restoration project: (1) do animals colonize restored habitat?, and (2) does the restored habitat meet the target animal's habitat requirements? Addressing these questions requires an understanding of how and why animals select specific habitats, including but not limited to mechanisms of navigation and cues used to locate habitat, characteristics of preferred habitat, resource requirements, and intra and inter-species interactions (Hale et al. 2020). Phenotypic variability in behavior (e.g., partial migration, see Bajer et al. 2015) within a population is another important consideration in habitat restoration, and restoration plans that accommodate and promote behavioral diversity (e.g., portfolio effect, see Schindler et al. 2015) may help increase the resilience of the target population to future perturbations.

Descriptive studies of behavior of fishes in the wild (e.g., Bergstedt et al. 2012; Binder et al. 2018) can help managers gain insight into the habitat preferences of species, but controlled experimental studies in both the laboratory and field tend to be better at identifying specific habitat cues, preferences, and behavioral mechanisms. For example, discrete choice experiments are commonly used to identify habitat preferences (e.g., Casterlin and Reynolds 1977; Brooker et al. 2013) and habitat-locating cues (e.g., Sorensen et al. 2005; Armstrong et al. In Press) in fishes. That said, results of laboratory studies should be applied to restoration projects with caution, as behaviors and preferences derived from controlled laboratory studies do not always translate to the wild. For example, Lake Trout in the field typically reside in water temperatures that are several degrees cooler than laboratory-derived thermal optima (Marsden et al. 2021). In general, a good approach may be to treat laboratory-based observations as hypotheses, and where time and resources allow, test them in the wild before initiating a restoration project. Behavioral studies can be costly and time and labor intensive, and often there is pressure to act immediately on restoration projects. However, failure to understand the behavioral ecology of a population in relation to habitat selection, especially colonization behavior and habitat preferences, could result in counterproductive or ineffective restoration efforts that could be even more costly in the long run.

Stock enhancement

Hatchery-based programs consisting of captive breeding or rearing of juvenile fishes for release to enhance or replace fish stocks for conservation or fisheries enhancement purposes have been applied throughout the northern hemisphere for well over a century, particularly with Salmonids (Naish et al. 2007). Despite considerable effort and investment, the effectiveness of stock enhancement programs at maintaining viable, naturally reproducing populations has been highly variable among species and systems (Fraser 2008). Hatchery rearing conditions can strongly influence the development of individual phenotypes, and one of the first experimental demonstrations of this phenomenon was the association between rearing density and physiological stress levels (Noakes and Leatherland 1977).

The epigenetic link between rearing conditions and phenotype spawned a thriving field of research into hatchery enrichment (Huntingford 2004). In general, enriched hatchery conditions offering greater structural complexity (Cogliati et al. 2019a), live prey in addition to commercial fish feed (Brown et al. 2003), realistic flow characteristics (Pedersen et al. 2008), and exposure to the outdoor environment under semi-natural conditions (Hatanpää et al. 2020) may provide valuable "life skills" training (Brown and Laland 2001; Hawkins et al. 2008) to fish prior to release. Enriched rearing has been associated not only with greater rates of survival (Alioravainen et al. 2018), growth (Vainikka et al. 2010), and performance (Hatanpää et al. 2020), but also migratory tendencies and phenologies more closely matching those of wild conspecifics (Hyvärinen and Rodewald 2013; Pedersen et al. 2008). Hatchery exposure to site-specific factors like biofilm communities and associated water chemistry may allow fish to "imprint" on their intended habitat and increase stocking success (Dittman et al. 2015; Putman et al. 2014a; Ueda 2011). Although fish released in better condition and at larger sizes generally experience higher survival rates and hatchery feeding regimes often allow individuals to reach satiation, food restriction immediately prior to release favors subsequent smoltification over precocious maturation in Atlantic Salmon (*Salmo salar*) parr (Vainikka et al. 2012).

Beyond hatchery influences on phenotypes of captive-reared Salmonids, behavioral interactions with other fish species at stocking sites can influence performance and survival of different phenotypes or strains of stocked fishes (Noakes and Curry 1995). Predation (Greenberg et al. 1997; Álvarez and Nicieza 2003; Kellison et al. 2003; Brokordt et al. 2006; Ochwada et al. 2009; Jackson and Brown 2011) and competition with both native (Miranda and Raborn 2013) and introduced (Scott et al. 2003) species, as well as between hatchery-origin and wild conspecifics (Yamamoto et al. 2008; Laffaille 2011), both negatively impact the success of stocking efforts and when they do not, stocked fish may impact the native population and community (Vehanen et al. 2009).

Collectively, conservation stocking studies have identified the importance of matching captive rearing conditions as closely as possible to natural conditions the fish will experience following release while limiting both rearing growth to ecologically realistic rates and competition for natural-type feed. This comes with the caveat that overfeeding and providing "too comfortable" an upbringing may mitigate the benefits of more enlightened rearing approaches. Despite the large body of work on this topic, long-term survival and fitness of stocked fishes remain largely unknown but the adoption of biologging and telemetry technologies (Ebner and Thiem 2009), as well as genetic techniques (Wilson et al. 2007; Fraser 2008) for long-term outcome tracking present great possibilities for future research. Further, more refined, genetically informed captive breeding programs (Lemopoulos et al. 2019) may be beneficial to both conservation-oriented stocking, as well as stock augmentations for recreational and subsistence fisheries (Dunham et al. 1986; Redpath et al. 2010; Blackwell et al. 2021; Vainikka et al. 2021).

The contributions of Dr. Noakes to fish behavior, conservation and management

Professor David Noakes was a pioneer in the behavior, ecology, and conservation of fishes. An extensive portion of the research contributions he made over five decades embodied the spirit of conservation behavior — with many of these contributions made well before the concept of conservation behavior was formalized. Consistent with Tinbergen's integrated set of explanations of behavior, Dr. Noakes research combined the principles and practices of animal behavior, endocrinology, physiology, ecotoxicology, morphology, genetics, and evolution to improve our understanding of fundamental questions about the biology of fishes in general, and salmonid fishes in particular (see Muir, this issue). Perhaps his greatest contributions, and most relevant to the theme of the current paper, came from Dr. Noakes' unyielding encouragement to integrate behavioral principles, practices, and understanding into management-scale studies exploring how fish populations respond to anthropogenic threats and identifying management interventions that could mitigate these threats.

As an ecologist and conservation behaviorist, Noakes' research on threats to native wild fish populations had mainly to do with such factors as habitat alteration or loss, effects of invasive species, and pollution (Table 1). His work on habitat alteration or loss tended to focus on how Salmonids used cover and natural areas of heterogeneity while foraging (Grant and Noakes 1986; McLaughlin and Noakes 1998), or during reproduction (Curry and Noakes 1995; Curry et al. 1995), and ultimately how these areas could be affected negatively by loss (Portt et al. 1986) or processes related to anthropogenic disturbance (Curry et al. 1994). Noakes and colleagues were also interested in understanding the impacts of pollution (Gunn and Noakes 1986, 1987) and invasive species on native biodiversity and the movement (Porto et al. 1999; Dodd et al. 2003; McLaughlin et al. 2006), spawning behavior (Scott et al. 2005b, c; Scanlan et al. 2018), and reproduction (Scott et al. 2003, 2005a) of natural populations. For example, he contributed early work demonstrating that Brook Charr (*Salvelinus fontinalis*) alevins showed behavioral avoidance of low pH and elevated aluminum levels and suggested that these behavioral mechanisms could impart an advantage in systems experiencing acidification (Gunn and Noakes, 1986).

From a management perspective, Noakes focused his research interests on management interventions that involved spatial planning and protected areas, restoring connectivity, and habitat and population restoration. For example, Noakes and colleagues investigated the effects of barriers on species richness (Porto et al. 1999; Dodd et al. 2003), and further, tested how eels use different locomotor behavior to overcome such obstacles (Linton et al. 2007). Additional work considered how Salmonids inherit magnetic maps to facilitate migration (Putman et al. 2014b) as well as aggressiveness, mobility, and trophic specialization to facilitate adaptation to diverse habitats and eventually, speciation (Ferguson and Noakes 1982, 1993; Skúlason et al. 1993). In other studies, Noakes investigated how behaviors, such as territoriality, limit population density and play a role in regulating the abundance of stream-swelling Salmonids (Cole and Noakes 1980; McNicol and Noakes 1981, 1984; Grant et al. 1989). Lastly, Noakes made significant contributions towards understanding how rearing conditions, captive-breeding, sensory biology, and fish community dynamics could influence population restoration efforts of Salmonids under diverse conditions (Noakes and Leatherland 1977; Noakes and Curry 1995; Scott et al. 2005a; Putman et al., 2013, 2014b; Dittman et al. 2015).

The contributions of David Noakes extend to most branches of fisheries biology and his accomplishments, particularly with respect to Salmonid ecology and biology are widespread. Much of his work has had a lasting impact on the fields of conservation behavior and animal behavior and will likely continue to do so for years to come.

The future of applied fish behavior through the lens of Dr. Noakes

Below, we briefly identify research directions that develop these approaches on subject areas close to Dr. Noakes' heart. We do so knowing that Dr. Noakes would actively argue for more integrative studies of conservation behavior in fishes that explore Tinbergen's four levels of explanation using novel conceptual and technical methods that on their own, or in combination with existing methods, reveal both greater and deeper understanding of behavior, and its connections to the life histories, ecology, and management for fish species of conservation concern.

Engaging in management scale experiments

One of the most common criticisms of research involving applied fish behavior and conservation behavior research more broadly (Caro 2007) is that the research is conducted at scales that are not relevant to managers. Because managers focus their efforts at the level of the population, and often across an entire waterbody, catchment, or land/sea-scape, studies that are exclusively conducted in the laboratory on a small number of fish without scaling up to field settings often fail to provide the information needed to influence policy and practice (Walters and Holling 1990). Even when work is done in the field, for example using telemetry, sample sizes are often small and may not be representative of the population (Brownscombe et al. 2017). As Director at the Oregon Hatchery Research Centre for the past decade, Dr. Noakes and his collaborators led a number of management scale experiments intended to support management and conservation decisions regarding fish. That work tested novel hypotheses, developed creative new tools, and gained insights into current fish management concerns largely associated with hatchery practices for conservation and hatchery production of wild Salmonid phenotypes (Cogliati et al. this issue). Prominent examples include research on early-life rearing (e.g., Cogliati et al. 2019a, b, c), breeding (e.g., Auld et al. 2021), imprinting (Dittman et al. 2015), and homing (e.g., Putman et al. 2013). These projects, some which continue today, involved extensive collaboration with management agencies and in situ testing of hypotheses relevant to native Salmonid conservation in the Pacific northwest. The scale of all of these studies was impressive in that they often combined laboratory studies with large sample sizes followed by releasing and tracking large numbers of tagged animals throughout their spawning migrations. Such work that bridges the lab and the field with large sample sizes and studies fish across large spatial scales over time are essential to generate actionable knowledge. This type of experimentation is also an important step for moving from a more descriptive applied fish behavior to a more predictive one that can inform management decisions. The work of Dr. Noakes provides a model for others to follow.

Conducting integrative research that bridges behavior and physiology

David Noakes appreciated that his two academic specialty areas, behavior and ecology, are essentially a seamless extension of an animal's physiology and anatomy. Physiological factors and mechanisms are the basis for motivating, controlling, and fueling behaviors (Breed and Sanchez 2010; Horodysky et al. 2015) (as a Ph.D. student Dr. Noakes was the teaching assistant in a class titled "Chemical Mediation"). Further, physiology along with anatomy is the basis for how a species determines its own ecological niche as described by Hutchinson (1958). It is therefore not surprising that his studies often included physiology. This research is relevant to a multitude of management and conservation topics. Physiological aspects of Dr. Noakes' research ranged from understanding physiological mechanisms driving or resourcing, i.e., bioenergetics (Cogliati et al. 2019c), behavior to whole animal physical and behavioral performance. The following are some examples to illustrate the depth and breadth of David's studies that had a physiological component. Much of his work centered around understanding movement of fish, often with a focus on migration and habitat selection. His approach working at the mechanistic level includes looking at downstream movement of juvenile Pacific salmonids as it relates to a fish's preference to be in salt water. That, of course, entails a shift in osmoregulatory physiology as the fish goes from a hydrating to a dehydrating environment. His ongoing projects involve clinical assessment of smoltification as they relate to movement behavior. Ion regulatory ability is key and can be influenced by stress that could affect behavior (Stewart et al. 2016, 2017). Visual isolation, as a consequence of structure in an environment, could also affect how fish respond to stressors and hence behavior (Cogliati et al. 2019b). Other studies explored how physiology is involved in fish social behavior (Noakes and Leatherland 1977). Physiology at the whole animal level includes questions such as how growth might be involved in juvenile salmon development and ultimately how that might affect migratory behavior (Self et al. 2018a, b). Studies concerning growth also have a strong bearing on conservation (Noakes et al. 1999). In addition, survival of out migrant salmonids appears to be different between the sexes (Thompson et al. 2015). In this regard, climate change and global warming potentially could affect sexual development in the fish (Cole et al. 2021). Acclimation temperature plays a role in how fish behave regarding different temperatures (Munakata et al. 2017). Orientation by adult anadromous salmonids concerns olfaction (Dittman et al. 2015). Upstream movement behavior in salmonids also involve gonadal factors; David's Master's student Eva Schemmel (Schemmel 2009) found that castrated steelhead had the same homing behavior as intact fish; swimming energetics was also not affected by castration. Whole animal response to contaminants reflects sensory physiology as well as behavior (Gunn and Noakes 1986). Whole animal physiology is also obviously also inherent in the research related to fish anesthetics mentioned earlier. Further, Dr. Noakes' studies related to magnetism as a guide for homing (Putman et al. 2013, 2014a, 2014b; Scanlan et al. 2018; Naisbett-Jones et al. 2020) is seminal both scientifically and for conservation and management. David assiduously contributed to our understanding of behavior and ecology by understanding that they could not be investigated on their own, but rather were best understood more holistically when physiology was included in his investigations.

Using technology to study applied fish behavior in the field

Technological advances and tool development in fields such as genetics/genomics (Hohenlohe et al. 2020), telemetry (Crossin et al. 2017), and electromagnetism (Klimley et al. 2021) have, and continue to, contribute to our understanding of animal behavior and in turn develop ideas and create solutions for many of the applied fisheries and conservation-based issues discussed in this paper. Dr. Noakes routinely pushed the frontiers of applied fish behavior using technology and was a champion for the development of tools that enabled behavior studies to be conducted in the field. Examples from early in his career included the validation and use of tissue concentrations of DNA, RNA, and proteins, and otolith ageing, to assess the growth rates of fish displaying different foraging tactics in the field and the nature of phenotypic selection acting on the fish (Locke 1995; McLaughlin et al. 1995, 1999). Today, advances in the field of genomics are creating opportunities to gain insight into the genetic makeup and relatedness of large numbers of individuals with greater accuracy and at a fraction of previous costs (e.g., De Coster et al. 2021). These advances have provided increasing insight into population genetics (Hohenlohe et al. 2020), animal movement, and migration (Cooke et al. 2008), and mating (Auld et al. 2019, 2021), which are all integral to the successful management and conservation of fish and fisheries. In the future, the complex and cumulative effects of anthropogenic stressors will make the use of these tools in isolation insufficient to address the fish, fishery, and conservation issues of the day. To deal with these issues, we need far-reaching collaborative and transdisciplinary studies involving trophic ecology, fish movement, and behavior as well as socio-economic and other human dimensions affecting fish and fisheries. Given the vast amount of data generated by new technologies, the challenge will be ensuring that it is analyzed in ways that will inform fisheries management and conservation decisions. Dr. Noakes was not a technology junkie — rather, he used the tool appropriate for the task at hand and always kept an open mind about how new tools could enable him to better address questions in applied fish behavior.

Conclusions

Our objectives herein were twofold, first to synthesize the knowledge and relevance of animal behavior to fishery management and conservation and second to view the current state of the disciplines through the lens of the late Prof. David L. G. Noakes, an influencer who advanced the field. It is clear that animal behavior has become a common and trusted tool in informing the management and conservation of fishes. Although such examples are rarely celebrated in the conservation behavior literature, they are well represented in the vast fisheries literature. Although once neglected (sensu Shumway 1999), behavioral tools and concepts are being used to understand the threats faced by fishes and to identify and refine management and conservation strategies. David Noakes was on the forefront of conservation behavior and proactive in incorporating fish behavior in management and management planning. His vision was remarkable, tackling many issues well before their time including the conflict between barriers for invasive species control in the Laurentian Great Lakes and their unintended consequences for native species and habitat connectivity—a critical global fishery issue now recognized as the connectivity conundrum (Zielinski et al. 2020). Likewise, his leadership at the Oregon Hatchery Research Center to confront the challenge of producing wild phenotypes in the hatchery is now beginning to change hatchery practices in the Pacific Northwest and has gained traction elsewhere. The primary behavioral research areas relevant to understanding threats to fish populations synthesized herein—habitat alteration and loss; exploitation; invasive species; pollution; climate change; protected areas and spatial planning; restoring connectivity; habitat restoration; and stock enhancement—are actively being pursued by a strong lineage of trainees mentored by Dr. David Noakes and his colleagues around the world. Noakes helped many find their niche in the science community; upon getting a manuscript rejected, he once said “just find a better journal.” In his dry, witty sense of humor, this meant you need to work harder to figure out where you and your work fit into the bigger picture and true to his mentoring style, he would facilitate the appropriate connections to make that happen. His passion, inspiration, teachings, and fortuitous (or cleverly engineered) introductions have led to a global network that continues to advance animal behavior and conservation behavior in fishery management and management planning. Looking forward, we submit that behavior is no longer neglected (Shumway 1999) when it comes to fish conservation and management which is in no small part to the work of Dr. David L.G. Noakes.

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