# The Movement Ecology of Fishes

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**Significance Statement:** Movement is rather ubiquitous for fishes across the globe. This synthesis explores this phenomenon and does so from a mechanistic perspective. Although the evidence base regarding the movement of fishes is vast, there are still a number of important knowledge gaps. Nonetheless, our understanding of fish movement is revolutionizing fundamental and applied ecology of fishes.

## Abstract

*Key words:* Movement ecology, movement ecology paradigm, spatial ecology, fish movement, dispersal, conservation, fisheries, management

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# I. INTRODUCTION

Fishes are unified in their ecology by a need to swim. From a small fish in a headwater stream to the largest fishes in the ocean, they need to move in order to find food, avoid predators, exchange gametes, and locate suitable habitat and environmental conditions that align with their life-stage-specific physiological tolerances and requirements (Smith, 2012; Secor, 2015). Because aquatic environments are inherently three-dimensional, movements can be in all directions, including vertically in the water column. Quite simply, fish are always on the move and the scale of such movements vary widely (Lucas & Baras, 2001; Secor, 2015). For example, some fish may engage in localized movements around a specific rock or coral head, whereas others may undertake vast transoceanic migrations. Some movements occur in a matter of seconds during a burst feeding event, whereas others may be diurnal, linked to seasonal phenomena, or life history transitions. Even fish that may be regarded as sedentary, such as those that live in burrows, move as they forage. For some fish, such as obligate ram ventilators, continual movement is needed to sustain life (Roberts, 1975). Although all fish move, many engage in migrations that are a phenomenon defined by their cyclical nature and fitness benefits (Dingle & Drake, 2007) such as moving from freshwater to saltwater or vice versa to seek out resources that are naturally dynamic over space and time (i.e., diadromy; McDowall, 1988; 2008). For the purpose of this paper we focus broadly on the movement of fishes (across all scales) of which some of said movements are considered to be migrations.

The movement ecology of fishes has long been of interest to ecologists and fisheries managers (e.g., Jones, 1968; Secor, 2015), but the fact that fish live in a watery world that is hostile to humans has made them difficult to study (Ogburn *et al*., 2017). Early research would involve using some form of visual ID tag to mark fish in one location with the hope of recovery later, thus providing information on movement (Nielsen, 1992). Although these approaches yielded some intriguing clues to the movement ecology of fishes, they were also misleading. In fact, for decades the restricted movement paradigm (Funk, 1957) was embraced by those working on fish in fluvial systems, where mark-recapture data revealed little evidence of movement. Further, those techniques were biased against the detection of larger scale movements. Only after electronic tagging and tracking methods (e.g., biotelemetry and biologging), that revealed larger-scale movements with greater accuracy were embraced, was the restricted movement paradigm largely abandoned (Gowan *et al*., 1994). Electronic tagging also revealed transoceanic movements by organisms such as bluefin tuna (Block *et al*., 2005), which was not only remarkable from an ecological perspective, but it also revolutionized their management (Kaplan *et al.,* 2010). The last few decades have seen a dramatic increase in the tools available to study the movement ecology of fishes (e.g., chemical tracers, electronic tags, image capture, associated quantitative analysis, and modelling tools) and consequently a phase shift in our understanding of their movement ecology. This is timely given that fishes in both marine (Crain *et al*., 2009) and freshwater (Reid *et al*., 2019) systems face many threats (e.g., fragmentation, climate change, overexploitation), such that it is necessary to understand how fish move throughout their aquatic world to inform management and conservation. Providing additional gravitas to this endeavour is the realization that migratory fishes are among the most threatened organisms on the planet according to the WWF Living Planet Index for the group (Deinet *et al*., 2020). Given collective interest in biodiversity conservation along with the many ecosystem services generated by fishes (Holmlund & Hammer, 1999), the ecology of fish movement is an important area of study.

Coincident with the increase in studies and knowledge about the movement ecology of fishes has been conceptual developments in the broader realm of movement ecology. Conferences focused on movement ecology, as well as the development of a journal by that name (i.e., Movement Ecology; see https://movementecologyjournal.biomedcentral.com/; Nathan & Giuggioli, 2013) reveal the level of interest and scholarship on the topic. Indeed, movement ecology is now considered an emerging discipline and is of interest to those working on many taxa including plants, insects, birds, and fish. Beyond the thousands of empirical studies that now exist on movement of various organisms, there have also been important theoretical and conceptual developments. Most notably was the development of a framework for movement ecology (Nathan *et al*., 2008; see below) that has been widely embraced (and cited over 2,000 times as of 2021). The framework provides a general unifying paradigm intended to place movement studies within a common context and advance the development of movement ecology as a discipline. In the words of the authors, the framework “integrates eclectic research on movement into a structured paradigm and aims at providing a basis for hypothesis generation and a vehicle facilitating the understanding of the causes, mechanisms, and spatiotemporal patterns of movement and their role in various ecological and evolutionary processes.”

Given the growing body of research on the movement ecology of fishes and both fundamental and applied interest in the topic, we provide a contemporary synthesis of what is known about the movement ecology of fishes. We adopt the well-known Nathan *et al*. (2008) movement ecology framework and consider how different components (e.g., external drivers, internal mechanisms) are relevant to fishes. To do so, we first introduce the framework and offer some refinements before exploring what we know about the different components as it relates to fish (see Fig. 1). We also consider the relevance of movement ecology to the management and conservation of fishes and identify future research needs and opportunities with particular focus on what the study of fish can bring to the emerging discipline of movement ecology (Holyoak *et al*., 2008; Schick *et al*., 2008). We do not dwell on the technological innovations that have enabled and advanced the study of fish movement as that has been explored elsewhere (e.g., Trueman *et al*., 2012; Hussey *et al*., 2015), but our approach is inclusive covering both freshwater and marine systems. We also consider movement in the broadest context meaning that we draw on examples beyond those fishes that undertake long distance migrations. Moreover, our approach is inherently multidisciplinary spanning ecology, ethology, endocrinology, biomechanics, environmental physiology, reproductive biology, sensory ecology, ecological modelling, resource management and applied science.

## II. The Movement Ecology Framework and its Relevance to Fishes

The movement ecology paradigm (i.e., Nathan *et al*., 2008) provides a framework of the causes and consequences of animal movement. The balance of expending resources to move against acquiring resources to grow and reproduce is fundamental to ecology, and much of the movement ecology framework has been established via the study of terrestrial animals that are easier to track because of the relative accessibility of land and the simple transmission of signals through air (Kays *et al*., 2015). For fishes, this framework has been widely applied to investigate the proximate and ultimate factors related to fish movement, but not adapted to more specifically address fish ecology (see Fig. 1). Herein we adopt the terminology used by Nathan et al. (2008) such as “internal state dynamics” and “external factor dynamics” for consistency but recognize that this terminology may not be uniformly embraced by the fish biology community. Details on the framework and the terminology can be found in the caption for Figure 1. Fishes are a highly diverse group of vertebrates that includes the cartilaginous, bony ray-finned, and bony lobefinned fishes. Among the world’s first highly mobile vertebrates, movement is fundamental to the ecology of all fish clades. Yet, the movement ecology of fishes is quite unique given the high diversity of body forms and habitats exploited by fish under the water. Immense efforts are underway to better understand fish movement, which would benefit from a comprehensive movement ecology framework of fishes.

The movement ecology framework points to the movement path, which for fish is a three-dimensional trajectory through space and time. The process that produces a given animal's path is a complex interplay of physiology, cognition, locomotory capacity, and other features captured in the paradigm (Nathan *et al*., 2008). Paths may be explained by external factors that occur over relatively short time scales such as temperature, water flow, lunar phase, and social context, among others. They may also be explained by internal factors such as endocrine, ontogenetic, genomic, or other factors of individual condition that can be collected when the animal is instrumented. Hypotheses relevant to where animals move (navigation) and how they move with respect to the speed or shape of the path can be inferred via comparisons between experimentally treated groups and controls (Birnie-Gauvin *et al*., 2020) or in a simpler observational and correlative framework. Electronic tagging has provided an exceptional tool to estimate fish paths in water, despite the many challenges associated with establishing precise positions in water. Serial estimation of positions from telemetry including radio, acoustic, or passive integrated transponders (PIT), as well as geolocators, allow investigators to see where and when fish are moving under the water. From these electronic tag data, investigators can attempt to resolve a path either finely, from triangulated data collected at short intervals (e.g., 2-120 s intervals), or coarsely, from detections once or twice a day (such as light-based geolocators that give sunrise and sunset positions).

Fish movement data have been summarised or estimated via numerous approaches such as network analyses (Jacoby *et al*., 2012; Lea *et al*., 2016), activity space estimators (Monk *et al*., 2017), selection functions (Griffin *et al*., 2021), Lévy walks or correlated random walks (Codling et al. 2008; Papastamatiou et al. 2013), Hidden Markov Models (Bacheler *et al*., 2019) or novel methods that integrate various modelling approaches (Lamonica *et al*., 2020). These models can be applied to reveal habitat associations, resource utilizations, and other features of the individual’s movement process that unravels the ultimate questions about movement: how it contributes to animal growth, survival, and reproductive output. A canonical example of using the movement ecology framework to relate movement to fitness includes the tagging of salmonids during the spawning migration (e.g. Cooke *et al*., 2014). Combining tagging with experimental manipulation (Birnie-Gauvin *et al*., 2020), non-lethal biopsy (Jeffries *et al*., 2014), or the use of tag sensors such as heart rate (e.g., Twardek *et al*., 2021) or acceleration (e.g. Burnett *et al*., 2014), allows direct inference of how movement processes affect animal fitness, albeit at brief timescales. Grasping how features of animal movement interface with animal fitness can then empower the use of movement models for conservation planning, fisheries management, habitat restoration initiatives, and more.

## III. The Environment

### *(1) Internal State Dynamics*

#### (a) Energy acquisition

On a fundamental level, fish must acquire more energy than they expend to allocate energy to growth and reproduction and achieve biological fitness (Brett & Groves, 1979). The cumulative capacity of individuals in a population to accomplish this ultimately determines population growth or decline (Tytler & Calow, 1985). Variation in fish size, activity level and efficiency, and life history strategy results in massive variability in energetic needs amongst fishes (Jobling, 1995). Aquatic environments often comprise a complex mosaic of potential energetic gains and costs that fish must navigate, through locomotion, to achieve positive net energetics. As such, locomotion is highly dependent on the often-transitory distribution of resources and environmental conditions in a fish's surroundings. Locomotion allows heterotrophs to obtain energy from their prey, and in theory, animals will target prey items that yield the highest foraging efficiency (i.e., the optimal foraging theory; Mittelbach, 1981). In terms of costs, locomotion often comprises a substantial portion of a fish's energy budget (Boisclair & Leggett, 1989) and as such, fish will seek to minimize their cost of transport within a landscape (Tucker, 1970; Shepard *et al*., 2013). Cost of transport, and therefore fish movement, is moderated by environmental factors such as water flow, water temperature, and even predator distribution (Clarke & Johnston, 1999; McElroy, Delonay, & Jacobson, 2012; Gallagher *et al*., 2017*a*). For instance, cyprinid migration patterns have been shown to closely follow fluctuating trade-offs between predation risk and foraging opportunities (Brönmark *et al*., 2008). Further, drift feeding fishes in lotic ecosystems or sharks in dynamic ocean currents take advantage of flow refugia to minimize energetic costs in high flow areas (Naman *et al*., 2019; Papastamatiou *et al*., 2021). Energy expenditure also scales positively with fish mass, and because fish are primarily ectothermic, it also scales exponentially upward with water temperature (Clarke & Johnston, 1999). For example, Pacific salmon will cease their migration and move into areas with cooler water to wait for thermal conditions that minimize energy expenditure (Keefer *et al*., 2018). Independent of movement, residing in an area with warm temperatures can have major metabolic costs that threaten fish fitness (Lear *et al*., 2020). Water temperature can also dictate access to certain resources, by excluding fish from nearshore foraging habitats where temperatures exceed a fish's physiological limits (Guzzo, Blanchfield, & Rennie, 2017).

Fuelled primarily by aerobic metabolism, the capacity of fishes to mobilize energy for movement, foraging, and digestion is influenced greatly by water temperature due to its impact on aerobic scope (Pörtner, 2010). There is some evidence that fish may selectively forage in locations (and at times) where temperature-driven aerobic scope is near optimal (Brownscombe, Cooke, & Danylchuk, 2017). Aerobic scope is a key factor in the capacity of fish to pass challenging water flows (Burnett *et al*., 2014) and to successfully complete long-distance migrations to spawning grounds (Eliason *et al*., 2011). Indeed, metabolic performance is suggested to constrain fish distributions due to temperature and oxygen distributions (Payne *et al*., 2016; Duncan *et al*., 2020). However, metabolic performance is not a universal predictor of fish behaviour (Clark, Sandblom, & Jutfelt, 2013), and there may be some balance between metabolic capacity to mobilize energy for activity such as moving (i.e., aerobic scope) with minimizing energetic costs (Halsey *et al*., 2018) or with meal size (Norin and Clark, 2017).

The link between environmental factors and fish energetics in determining fish movement and distribution are also supported by modelling exercises. Energetics can form a key mechanistic basis for estimating movement patterns and responses to environmental changes such as warming climate (Malishev & Kramer-Schadt, 2021), and as a performance-based predictor of fish habitat suitability (Del Raye & Weng, 2015). As a key currency of life, energy has a clear connection to fish movement ecology, and serves as a valuable metric for describing fish movement patterns and distributions. There are still some important unknowns about how commonly and in which ecological contexts energy conservation and/or metabolic performance actually dictate fish movement behaviour and fitness, as well as trade-offs with other constraining factors (e.g., predation risk, other measures of physiological performance such as osmotic regulation capacity; Brownscombe et al. 2022). that may be resolved with further research on this topic to develop mechanistic models of fish movement.

### (b) Endocrine State

Determining the proximate and ultimate drivers of movement in fishes is inherently difficult given the panoply of interactions within and among individuals and populations, and their abiotic environment (Drakou *et al*., 2009; Rasmussen & Belk, 2017). In addition, interactions between external (e.g., environmental cues) and internal (e.g., variables dependent on the condition of the individual) factors can certainly occur and it can be difficult to isolate causality (Clobert *et al*., 2012). In fish, physiological traits that have been linked to movements include behavioural tendencies, body condition and size, sex, and the stage of development (e.g., ontogenetic shifts), as well as endocrine state (Rasmussen & Belk, 2017). Defined as any tissue or cell that releases a hormone directly into the bloodstream, signalling or inducing a physiological response in some target tissue, the endocrine system is essentially a control system that responds to both internal and external signals (Blanton & Specker, 2007). The hypothalamus-pituitary-endocrine gland axis functions by responding to signals from the central nervous system (CNS) and converting them to hormone messengers that act on individual glands like the gonads (i.e., the hypothalamus-pituitary-gonadal axis) or the thyroid (i.e., the hypothalamus-pituitary-thyroid axis; Kloas *et al*., 2009). When triggered by stimuli from the CNS, the hypothalamus secretes releasing factors that act on the pituitary, resulting in the pituitary releasing tissue-specific hormones (e.g., thyroid-stimulating hormone to the thyroid, luteinizing or follicle-stimulating hormones to the gonads, growth hormones to the liver and gonads, adrenocorticotropic hormone to interrenal cells) into blood circulation (see Kloas *et al*., 2009).

There are several key examples of laboratory and field approaches to isolating the endocrine system’s effects on fish movement. The reproductive process and associated seasonal movements in fishes are cyclical, regulated by environmental factors like photoperiod, water temperature, and water flows (Lucas & Baras, 2001). The fish's brain perceives relevant environmental (and/or sometimes social) cues, and initiates a physiological response whereby the brain activates the pituitary and triggers changes in the gonads to initiate steroidogenesis (i.e., sex steroids, like testosterone [T], 11-ketotestosterone [11-KT], and estradiol [E2]) and gametogenesis (Servili *et al*., 2020). Determining if sex steroids trigger spawning movements themselves remains unclear. However, T, 11-KT, and E2 appear to regulate both upstream and downstream migratory behaviours in masu salmon (*Oncorhynchus masou*; Munakata *et al*., 2011). Somatic hormones have also been implicated in fish movements. Ojima & Iwata (2009) documented that growth hormone-releasing hormones triggered downstream movement of chum salmon (*Oncorhynchus keta*) fry. A surge in thyroid hormones (TH) during the parr–smolt transformation was associated with physiological changes during downstream migration, such as the acquisition of negative rheotaxis (Specker *et al*., 2000). In a review by Iwata (1995), treatment of the thyroid hormone Triiodothyronine (T3) to chum salmon fry changed their swimming direction from upstream (against flows) to downstream (with flows), and Edeline *et al*. (2005) showed TH to be involved in the regulation of glass eel (*Anguilla anguilla*) locomotor activity where thyroxine (T4) and thiourea (TU) treatments increased and decreased locomotor activity, respectively. Edeline *et al*. (2005) suggested that TH likely affect fish activity and locomotion through an activation of cellular metabolic pathways, though they explain that the precise physiological mechanisms that alter locomotion remain unclear. "Hunger" is perhaps one of the clearest examples of a driver of movement that is inherently and distinctly intrinsic. Hunger stimulates a fish's movement in search of food and is primarily regulated by the neuroendocrine system (Fletcher, 1984), and in particular by the peptide hormone ghrelin. There is much evidence that ghrelin is orexigenic (i.e., an appetite stimulant) and has generally been accepted as a "hunger hormone" (Higgins *et al*., 2007; Jönsson, 2013; though see Jönsson *et al*., 2010 for conflicting results in juvenile rainbow trout *Oncorhynchus mykiss*). In male smallmouth bass (*Micropterus dolomieu*), ghrelin levels were lowest during the parental period when they cease foraging to defend their nest and brood; plasma ghrelin levels increased near the time when fry achieved free swimming, and males subsequently left to actively forage again (Hanson *et al*., 2009). Similarly, ghrelin appears to increase swimming (foraging) activity in brown trout (*Salmo trutta*) as a result of increased feeding motivation (Tinoco *et al*., 2014).

Mechanistic links between movement and internal physiological status remains one of the largest knowledge gaps in fish movement ecology (Lennox *et al*., 2019b). We note that several key hormones (like the sex steroids listed above) have been well studied and provide a template for investigating the role of hormones in movement, although causality can be challenging to ascribe without rigorous experimentation. Moreover, generalizability of hormone function across fish taxa is tenuous without multi-species studies. Many avenues exist to better understand internal drivers of movement, for example blood samples drawn from fish can be analysed for circulating hormones and then linked to movements by video analysis in laboratories or by telemetry in the field, with randomized control treatment experiments with hormone or hormone blocker implants used to establish causal links. Endocrine experiments, such as those listed in the examples above, revealed how the endocrine system can act as the ultimate driver of fish movement and that the delivery of hormones through the fish's organ network directly informs the movement process. In a changing world, fish responses to stimuli may become altered by environmental pollution (Affandi & Ishak, 2019) or maladaptive as novel environments emerge (Lennox *et al*., 2020). A better understanding of how the endocrine system functions to control fish behaviour is therefore crucial knowledge that can be used to manage the environment and track consequences of macrophysiological trends in fish populations (Jeffrey *et al*., 2015).

### (c) Maintenance of Homeostasis

Homeostasis – the maintenance of a consistent internal state – is a somewhat misleading concept, at least for some aspects of the internal state (physiology) of fishes. Schreck (2010) argued it is more constructive to adopt the concept of allostasis – achieving stability through change. Either way, in these contexts, the hypothalamic-pituitary-interrenal (HPI) axis that regulates stress in fishes is a useful physiological system from which to understand how fishes integrate information from their surroundings and their internal state. Stress, which can be acute or chronic, involves the release of stress hormones that enable the animal to perform in or escape from challenging circumstances (e.g., hypoxia, predation risk, low food availability). There is a body of research about how stress – which is ultimately meant to facilitate a return to or maintenance of homeostasis – can directly affect behaviour and therefore, presumably, movement of wild animals. However, we have no electronic tags yet that allow us to measure stress directly in situ. There is literature on the interplay between stress and behaviour based on laboratory experiments from which one could make predictions about how wild fish might behave; testing those predictions in the wild however, is a challenge. One approach that has been used is to biopsy fish when they are caught for telemetry tagging, to assess their level of stress (defined broadly) and then examine how physiological indicators of 'stress' predict subsequent movement and survival (e.g., Cooke *et al*., 2006; Crossin *et al*., 2009).

Cortisol, the main stress hormone in fish (noting that cortisol also has many other roles), can be measured from a small blood sample, and has been linked to the timing and success of seaward migration in acoustically-tagged sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). Individuals with elevated cortisol levels (high stress) exited fresh water earlier – perhaps to escape stressors (i.e., predation, low energetic resources) – but were less likely to survive their migration (Birnie-Gauvin *et al*., 2019). Other types of stressors have also been linked to changes in movement. For example, pathogens and disease burden have been found to decrease diel movements in a coral reef fish (French grunt, *Haemulon flavolineatum*; Welicky & Sikkel, 2015). In the high seas, trawl surveys and environmental monitoring data have shown that dissolved oxygen greatly affects the distribution of demersal species, likely as these fish attempt to stay within conditions they can tolerate well (Pihl *et al*., 1991; Sobocinski *et al*., 2018). Sea lice infections cause salmonids to return to fresh water earlier in an attempt to shed the marine parasite (Halttunen *et al*., 2018) – it is likely that the HPI axis plays a role in regulating movement in cases like these. In Pacific salmon undergoing spawning migrations, cortisol has been measured in telemetry tracked fish but typically has been found to be associated with survival (i.e., migration failure) rather than differences in behaviour and movement per se (e.g., Cooke *et al*., 2006; Crossin *et al*., 2009; Cook *et al*., 2014). Fisheries interactions can also activate the stress axis to promote refuge-seeking (Cooke *et al*., 2014; Brownscombe *et al*., 2014). In essence, fish may move (or not) when homeostasis is disturbed, or to avoid disturbing a state of homeostasis.

### *(2) External Factor Dynamics*

#### (a) Biotic Drivers

Movement processes of individuals can be influenced by intraspecific and interspecific interactions (reviewed in Shaw, 2020). Across this spectrum, biotic factors including competition for resources (e.g., space, food, and mates), and predator-prey relationships can mediate how an individual fish moves through space and time (Shaw, 2020), as well as how and when an individual switches between movement states (Russell *et al*., 2017). Individual-level variation in movement patterns can lead to distinct structure of populations through social interactions (Jolles *et al*., 2020), and be moderated by a range of sensory stimuli via visual, tactile, mechanosensory, auditory, electroreception, and chemical cues (Gammon *et al*., 2005, Butler & Maruska, 2018). For example, Gammon *et al*., (2005) showed that inter-sexual and intra-sexual pheromones of reproductive male round goby (*Neogobius melanostomus*) influenced the swimming velocity and directed movement of females. Dominance hierarchies linked to factors such as body size, sex, and condition can also influence the scope and outcome of intraspecific social interactions, and subsequent variation in movement patterns among focal individuals (Freeman & Stouder, 1989). For example, Freeman & Stouder (1989) showed that body size influenced the outcome of intraspecific interactions and subsequent depth distribution in streams for mottled sculpin (*Cottus bairdi*).

The individual movement of fishes is both a driver for - and consequence of - competition, and thereby can be viewed as an important component of the overall movement ecology of fishes. Foraging decisions are profoundly influenced by competition, where the distance and scale of movement of individuals can be driven by the density and abundance of overlapping consumer species. On coral reefs, where competition is high and fish are site-attached, an increased abundance of one parrotfish species (*Scarus* spp.) was shown to reduce the foraging range of another parrotfish species (Nash *et al*., 2012). Coastal and estuarine shark species commonly co-exist in competitive aggregations, such that large and small individuals and species may overlap and vie for access to food resources. Under competitive situations, larger shark species exhibited a reduction in activity space and habitat use, whereby smaller individuals increased their activity space and were pushed out to avoid predation (Heupel *et al*., 2019). Among larger predatory fishes, it has been assumed that subtle changes in individual distribution, as well as dietary specificity, drive resource partitioning that may explain competitive coexistence (Gallagher *et al*., 2017*b*; Papastamatiou *et al*., 2018*a*). Pulses in ephemeral or opportunistic resources offer large predatory fishes valuable energetic incentives to scavenging, but at the cost of acutely intense competition. Competition for access to prey-rich subsidies on dead whale carcasses, for example, has been demonstrated to profoundly alter the distribution of white sharks (*Carcharodon carcharias*) over short temporal scales, bringing together upwards of 40 sharks at a time (Fallows *et al*., 2013). The manner in which these large sharks compete for access to the carcass – and whether they are energetically rewarded – will in turn shape their foraging decisions and migrations for periods of weeks to months (Fallows *et al*., 2013).

Competition for space can also drive the success of important life history events tied to movement, such as the homing migrations of anadromous fishes. Swimming behaviour in upward-migrating sockeye salmon (*Oncorhynchus nerka*) changes as individuals compete for access to the best river microhabitats, which optimize speeds and reduce transport costs (Hanson *et al*., 2008). In many freshwater lakes, centrarchid fishes share a similar spatial distribution, such that space for feeding and nesting are at a premium. Competition for these resources results in sympatric species, such as bluegill (*Lepomis macrochirus*) and pumpkinseed (*Lepomis gibbosus*), partitioning their home ranges between littoral and pelagic zones (Mittelbach, 1984). In riverine habitats, competition between these two species resulted in opposing patterns of diel activity, whereby bluegill were more active during the night, and pumpkinseed increased their activity during daylight hours (Klinard *et al*., 2018). The effects of competition on fish movement clearly vary among and within species, and will also be influenced by internal state and the physical environment, thereby serving as a unifying moderator of fish movement ecology.

A considerable amount of attention has been paid to the dynamics of schooling behaviour (i.e., the coordinated movement of fish, often of the same species) in fishes, where traits such as mutual attraction, unitary orientation, and synchronization among conspecifics influence movement patterns of individuals within a school (reviewed in Pavlov & Kasumyan, 2000). Fish distribution within schools can be dynamic, with the movement of a focal individual being driven by the behavioural response of others in the school, and how related interactions are influenced by sensory stimuli, motivations, and risks (Pavlov & Kasumyan, 2000). Throughout their lives, fish must balance resource acquisition, whether for energy or mates, with the potential risk of predation (Lima & Dill, 1990; Brönmark *et al*., 2008). Schooling behaviour in response to predation pressure has been studied extensively in guppies (*Poecilia reticulata*), with researchers finding that whereas individuals from low and high predation risk populations did not differ in their number of movements within an experimental school (Ioannou *et al*., 2017), those from high predation risk populations did school more tightly, were more strongly socially connected with their neighbours in the school, and maintained schools longer than individuals from low predation risk populations (Kelley *et al*., 2011). Similar to guppies, minnows (*Phoxinus phoxinus*) exposed to northern pike (*Esox lucius*) modify their movements from dispersed to compact schools, but save their most energetically costly evasive movements for when the pike strikes the school (Magurran & Pitcher, 1987).

Changes in habitat selection and the spatial extent of habitat use are two other common responses in fish to the presence or perceived presence of a predator. When exposed to potential predators, fish, such as convict cichlids (*Archocentrus nigrofasciatus*), slimy sculpin (*Cottus cognatus*), Chinook salmon (*Oncorhynchus tshawytscha*), and Atlantic salmon will significantly reduce their movements over time and space or slow down their migrations (Bryer *et al*., 2001; Brown *et al*., 2006;, Ylönen *et al*., 2007; Wisenden *et al*., 2008; Kim *et al*., 2011; Sabal *et al*., 2020). In contrast, killifish (*Rivulus hartii*) in rivers increase movement in areas where predators are present (Gilliam & Fraser, 2001). Other species will ‘freeze’ (Becker & Gabor, 2012) or seek shelter (Brooker *et al*., 2013, Gotceitas & Godin, 1991) when presented with predators. In coral reef fish, like the filefish (*Oxymonacanthus longirostris*), the need for refugia access in high branching corals can often lead to selecting against higher quality food patches (Brooker *et al*., 2013). Small juvenile lemon sharks (*Negaprion brevirostris*) have been shown to modify their depth use, selecting for shallow water habitats and moving with the tidal swing to avoid encounters with larger bodied, sub-adult lemon sharks (Wetherbee *et al*., 2007; Guttridge *et al*., 2012). They may also use mangrove prop root complexity for shelter (Guttridge *et al*., 2012). Some fishes, particularly those in tropical marine environments with access to complex coral reef and reef adjacent habitats, undergo ontogenetic changes in movement patterns and habitat use, in part to minimize exposure to potential predators (Grol *et al*., 2014).

Another method to minimize predation risk is modifying the timing of movement, with many fishes, spanning from sockeye salmon to blacktip sharks (*Carcharhinus limbatus*), migrating (Keefer *et al*., 2013; Furey *et al*., 2016) or expanding activity space and habitat use (Grol *et al*., 2014; Legare *et al*., 2018; Rooker *et al*., 2018) during crepuscular periods and at night to minimize detection from visual and diurnal predators. Another strategy, similar to schooling, is to synchronize the timing of migration to effectively swamp the predators, collectively increasing the chance of survival (Furey *et al*., 2016). Finally, migration on its own can be a strategy to avoid predation. Roach (*Rutilus rutilus*) have been documented to migrate seasonally from lakes with high predation pressure from northern pike and European perch (*Perca fluviatilis*), but also abundant food sources, in the summer, to habitats with fewer predators and reduced food availability in winter when growth is inherently slower due to cold temperatures (Brönmark *et al*., 2008).

### (b) Abiotic Drivers

External factors play a key role in determining the activity and behaviour of all animals, including fishes (Holyoak *et al*., 2008). Forces underlying the choice of whether to move or stay can be categorized broadly into proximate and ultimate factors. Proximate abiotic factors drive movements related to physiological optima or constraints and explain why an organism moves for specific short-term payoffs, whereas ultimate factors are selective forces that drive adaptation and specialization. While sometimes difficult to distinguish (Nathan *et al*., 2008), proximate and ultimate factors can be understood easily if contextualized together. For example, changes in light intensity (proximate factor) triggers diel vertical migration as a means to increase feeding opportunities or to avoid predators, which ultimately increases fitness (Mehner, 2012). If movements are timed incorrectly and fish become decoupled (i.e., mismatch) from critical abiotic conditions, fitness may be jeopardized (Forrest & Miller-Rushing, 2010; Miller-Rushing *et al*., 2010). As such, and considering the diversity of fish movement strategies (Lowerre-Barbieri *et al*., 2019), fish use multiple sensory inputs to detect changes in their environment (Huijbers *et al*., 2012), and may respond to a single factor with considerable influence on physiology (e.g., water temperature) or to combinations of environmental correlates (e.g., seasonal changes or acute disturbance events). Here, we characterize several key abiotic factors that can influence a fish's motivation and capacity to move, and have direct implications on fitness (e.g., energy acquisition or reproduction).

As obligate poikilothermic ectotherms, temperature is the master controlling factor of fish physiology (Brett, 1971; Beitinger & Fitzpatrick, 1979). Except for thermo-conserving tunas and sharks (Bernal *et al*., 2001), external temperature will affect metabolic rate in the vast majority of species regardless of thermal tolerance, climatic adaptation, ontogeny, and body size (Clarke & Johnston, 1999; Comte & Olden, 2017). Generally, fish seek the appropriate thermal niche, where temperatures are optimal (Beitinger & Fitzpatrick, 1979; Magnuson, Crowder, & Medvick, 1979; Jobling, 1997). Behavioural thermoregulation is theoretically necessary to maximize growth, which has been demonstrated in the field and lab (Jobling, 1997; Haesemeyer, 2020). For example, behavioural thermoregulation plays out strikingly where thermal gradients form, and fishes aggregate according to thermal preference (Sogard & Olla, 1998; Humston *et al*., 2000; O'Gorman *et al*., 2016; Andrzejaczek *et al*., 2019), or aversive temperatures interrupt migrations (Reynolds, 1977; Goniea *et al*., 2006). However, temperature cannot always explain acute movements (Vollset, Fiksen, & Folkvord, 2009; Raby *et al*., 2018). For instance, the lag time to equilibrium between external temperature and deep tissue allows fish to foray into otherwise sub-optimal environmental conditions for the purpose of feeding or predator avoidance (Sogard & Olla, 1998; Mehner, 2012), followed by a return to preferred conditions (Sogard & Olla, 1998; Sims *et al*., 2006; Papastamatiou *et al*., 2015). Phenotypic plasticity seems to allow populations to adapt to local thermal conditions (Stitt *et al*., 2014; Corey *et al*., 2020), underscoring the genetic component to thermal tolerance in fishes (Meffe *et al*., 1995).

Teasing out the effects of singular variables, such as water temperature, is challenged by strong collinearity with additional variables expected to influence movement (Currey *et al*., 2015). For example, within the epipelagic area, studies have shown that the interaction between temperature and dissolved oxygen availability likely drives the horizontal and/or vertical space use of large fishes (Carlisle *et al*., 2017; Coffey *et al*., 2017; Andrzejaczek *et al*., 2019; Duncan *et al.,* 2020). In another example, Childs *et al*. (2008) found that spotted grunter (*Pomadasys commersonnii*) were tolerant to a wide range of environmental conditions, yet moved in response to large fluctuations in salinity, temperature, and turbidity. Synergistic effects of environmental variables complicates how movement is associated with changes in water temperature. Glass-phase

European eels traverse estuaries using selective tidal stream transport in which orientation and directionality is primarily driven by salinity gradients and olfaction, but temperature contributes to the synchronization of activity with tidal cycles and in the switch from estuarine to riverine migration strategies (Edeline, Dufour, & Elie, 2009). Welsh & Liller (2013) showed that yellow-phase American eel (*Anguilla rostrata*) upstream migration is driven by additive effects of river discharge and water temperature, depending on time period. Even with an acute movement resulting from a distinct disturbance event, like that of an extreme weather event (e.g., from a large storm or hurricanes), it remains challenging to decipher the exact set of abiotic factor(s) (e.g., barometer, wind intensity or direction, temperature change) that trigger refuge-seeking movements (Secor *et al*., 2019; Massie *et al*., 2020; Gutowsky *et al*., 2021). Changes in abiotic conditions can also alter the volume of habitat available and its relative "useability", which can necessitate fish movement (e.g., searching for alternative habitats; e.g., Dare *et al*., 2002). Collectively, understanding the specific role of any individual abiotic variable on movement is challenging because the roles and influences of any one factor will vary among taxa, populations, life stages, or environments, and because complex interactions and correlations exist among factors, such as water temperature, dissolved oxygen, salinity, olfactory chemical cues, currents/flows and tides, lunar cycles, photoperiod, and circadian rhythms (Kuparinen, O'hara, & Merilä, 2009; Forsythe *et al*., 2012; Schlaff, Heupel, & Simpfendorfer, 2014; Stich *et al*., 2015; Nakayama *et al*., 2018; Thiem *et al*., 2018).

## IV. The Individual

### *(1) Navigation Processes and Capacity*

All behavioural decisions of fish, including orientations (which involves the ability to move in a given compass direction), movements, and migrations, are in response to cues detected and processed by neurosensory systems that represent a transfer function between environmental parameters and individual behaviours (Weissburg & Browman, 2005). Navigation in space and time (which is the ability of an organism to locate its position and use that knowledge to inform where it wants to go) requires an individual to sense and respond to information about the spatiotemporal structure and dynamics of the environment, often including information about the behaviour and location of conspecifics or other species (Nathan *et al*., 2008). A mechanistic understanding of movement ecology considers the following tenets: (i) individuals experience only their local environment as delimited by their various sensory abilities under the current physicochemical conditions, and (ii) individuals can only prefer an environmental variable they can sense and where there is a direct relationship between a sensory receptor and/or afferent nerve activity and the physical variable (Horodysky *et al*., 2016). The behavioural decisions of each individual to maximize its fitness in response to its internal physiological state thus iterates across individuals to become the ecologies of populations (Horodysky *et al*., 2015).

Fishes migrate throughout the world's oceans, within lakes and rivers, and between these water bodies (Lennox *et al*., 2019b), suggesting the involvement of a myriad of physiological responses to many sensory stimuli. Collectively, the studies of fish movements, migrations, and navigation processes comprise a broad field that has been fairly well-studied, though many interesting questions remain (Dittman & Quinn, 1996; Kingsford *et al*., 2002; Hinch *et al*., 2006; Putman *et al*., 2014). This section therefore focuses on the narrower topic of the sensory multimodality required to navigate on both large and small scales. Orientational and navigational cues that can be used for long periods of time over travel distances of thousands of kilometres may differ from those that are most useful over limited spatial scales (e.g. a few km) and short time-scales from seconds to hours (Mouritsen, 2018). Fish movements thus most likely involve interpreting multimodal sensory information from magnetosensory (in species possessing this ability), chemosensory, and photosensory systems that may change with distance and duration to the target destination. Questions remain about how several environmental cues are used together during a given phase of movement/migration as well as how neural processing transitions between phases (Mouritsen, 2018).

Most distance-migrating fishes likely use a biphasic navigational strategy. It is well documented that salmonids use chemical cues to identify their natal streams at the end of spawning migrations, with brain–pituitary–thyroid hormones playing important roles in olfactory memory formation in downstream-migrating rheotactic smolts and brain–pituitary–gonadal hormones assisting adults in their retrieval during upriver migration (Hasler & Scholz, 1983; Dittman & Quinn, 1996; Bett & Hinch, 2016; Ueda, 2018). Catadromous anguillid eels (Barbin *et al*., 1998) and anadromous clupeids (Dodson & Dohse, 1984) also appear to use olfactory cues to direct migratory movements. As a consequence of dilution and currents, however, olfactory cues alone are insufficient to influence migrations that can span upwards of a thousand kilometres from the open ocean to near-coastal waters or vice versa (Lohmann & Lohmann, 2019). Long distance migrations, such as those undertaken by various salmonids, thunnids, as well as anguillid eels, are presumably initiated by geomagnetic sense, as well as environmental cues, and are possibly further enhanced by the use of celestial and visual cues, such as the sun compass and the polarization of light (Hawryshyn, 1992; Parkyn *et al*., 2003; Naisbett-Jones *et al*., 2017). In relation to the lifetime of most fish, the Earth's geomagnetic field may serve as a reasonably constant and reliable source of directional and positional information (Formicki *et al*., 2019), that exists everywhere on Earth, is present day and night, and largely unaffected by weather (Johnsen *et al*., 2020).

Diverse mechanisms have been proposed as the basis for detecting magnetic fields: electromagnetic induction (possible in elasmobranchs via the ampullae of Lorenzini), magnetic-field-dependent chemical reactions (hypothesized in terrestrial vertebrates), and biogenic magnetite crystal-based magnetoreception (hypothesized in fishes in which magnetite crystals have been found, such as salmonids; Johnsen & Lohmann, 2005). However, secular variation of the Earth's magnetic field over time and the small magnitude of magnetic signals relative to thermal and receptor noise would compromise fine-scale navigation required to locate imprinted, high-specificity natal sites in long-lived species (Putman *et al*., 2013; Johnsen *et al*., 2020). Therefore, as adult salmon narrow their movements to coastal waters in the vicinity of natal waterways, olfactory chemical gradients, visual landmarks, and soundscapes become increasingly important cues that allow fish a fine-scale resolution to pinpoint their final destinations for spawning migrations (Lohmann & Lohmann, 2019; Mouritsen, 2018). It is perhaps not surprising that many migratory fishes thus move en masse, potentially benefiting not only from their own sensory information, but also from the collective "intelligence" of the group's behaviour, at least in certain circumstances (Couzin, 2009; Berdahl *et al*., 2013; Berdahl *et al*., 2016; Berdahl *et al*., 2018). Collective sensing demonstrates how social interactions, individual state, environmental modification and processes of informational amplification and decay can all tune adaptive responses that affect movements by averaging over error-prone individual directional estimates (Berdahl *et al*., 2013). For example, in migrating anadromous salmonids, collective navigation may facilitate passage of fish through complex anthropogenic barriers such as fishways and dams en route to their spawning grounds (Okasaki *et al*., 2020).

Navigational cues can also direct recruitment processes and settlement in larvae and juvenile fishes. Specifically, sockeye salmon demonstrate eight migratory phases in their life cycles, five that occur in fresh and brackish waters prior to sexual maturity and appear to be influenced by primarily visual and hydrodynamic cues (reviewed in Hinch *et al*., 2006). Larvae of many coral reef fishes use an innate celestial and magnetic compass direction to locate the general vicinity of the reef, then olfactory and/or auditory cues to refine the reef's location, and finally vision to locate a suitable microhabitat within the reef (Gerlach *et al*., 2007; Radford *et al*., 2011; Mouritsen *et al*., 2013). Like natal rivers, individual reefs may have distinctive olfactory, visual, and auditory signatures that fish may imprint upon at hatching or during the early stages of larval transport (Atema *et al*., 2015). Mechanistic studies of the sensory abilities of fishes and the stimuli produced by natural reefs may thus be of more than simple academic interest in the ecological restoration of reefs (Gordon *et al*., 2019).

Collectively, improved understanding of the roles of sensory systems for orientation and navigation of larvae and adults remains an exciting field for future study, providing mechanistic insights into the evolutionary drivers of fish dispersal strategies (see Radinger and Wolter 2014), as well as the physical and physiological bounds of migration potential in the Anthropocene's human-altered ecosystems. Understanding the role of fish sensory biology in movement ecology is also critical for effective fisheries management as it provides tools necessary to: (i) interpret behavioural responses both at the individual and population level, (ii) suggest approaches to modify behaviours (most relevant to directing fish migrations in the presence of anthropogenic structures), and (iii) ultimately predict population-level consequences associated with natural and anthropogenically-induced environmental changes (Madliger, 2012; Blumstein & Berger-Tal, 2015; Horodysky *et al*., 2016).

### *(2) Motion Processes and Capacity*

Adaptive selection has acted through ecology and environment impacting body form and functional diversity in fishes. Fish are both constrained and enabled by their anatomy and thus have different ways of swimming that influence their success in different habitats. Broadly, steady swimming styles can be categorized as body-caudal fin swimming (body and caudal fin are primary propulsors) or median/paired fin swimming (dorsal, anal, pelvic or pectoral fins are primary propulsors; Breder, 1926; Lindsey, 1978; Webb, 1975). Within these overarching categories, there are unique swimming modes that are particularly suited to each species' ecological niche, life history, and body shape. For example, species that make long distance migrations or are high speed specialists use swimming styles that prioritize thrust production (e.g. salmonids - Webb *et al*., 1984 and thunnids - Dewar & Graham, 1994), are often streamlined, and may have muscle arrangements that keep muscles at an optimal operating temperature (e.g. tuna red muscle is close to the vertebral column to insulate it from the water; Carey *et al*., 1966), and/or muscle fibres that are optimized for endurance swimming (e.g. a higher proportion of red fibres laterally and red fibres spread throughout the white muscle in salmonids; Johnston *et al*., 1975). Conversely, for species where it is more important to be manoeuvrable (e.g. reef fish), body shape enhances manoeuvrability and non-caudal fins are relied on more heavily for regular locomotion to allow the fish to generate de-stabilizing thrusts that facilitate efficient turning for weaving in and out of complex habitat (Webb, 2005).

Fish have one of the most unique vertebrate body muscle architectures, including nested cones of white (high force, easily fatigued, fast contracting) muscle and a narrow, laterally positioned strip of red (low force, fatigue resistant, slow contraction) muscle (Shadwick & Gemballa, 2005). This placement of red muscle maximizes mechanical advantage, while helical white fibre trajectories maintain a relatively constant level of bending along the body, and the sheer volume of white muscle make this organization effective at a variety of speeds. The muscles of median and paired fins are a mixture of white, red, and pink (physiological properties intermediate between red and white) fibres (Drucker *et al*., 2005). Selective activation of muscle fibre subsets allows pectoral fins to be used for a variety of tasks including acceleration, steady swimming and turning. Fish make use of the body and fins selectively depending on the task or environment. A fish swimming slowly only recruits red body muscle and/or median and paired fins, while the white muscle remains largely inactivated. As speed increases (or during acceleration or escape), white muscle is recruited. Navigating complex three-dimensional environments can be accomplished either through slender, flexible bodies, or by paired or median fins that increase manoeuvrability and fine tune roll, pitch, and yaw (Drucker *et al*., 2005).

Independent of body shape, abiotic environmental factors such as temperature, pH, and salinity can influence muscle contraction physiology, affecting the rate of cross-bridge cycling and oxygen availability, and therefore the capacity of a muscle to produce force (see Section 3.2 – External Factors). At cold extremes (especially in larval fish), there may be some influence of the increased viscosity of the water on the ability of fish to produce force for locomotion. On larger spatial scales, any change in the connectivity of a habitat, natural or manmade, will influence the ability of a fish to move freely, whereas pollution, water chemistry, and turbidity changes may influence the ability of the sensory system to access critical information for swimming performance (see Section 4.1 – Navigational Processes and Capacity).

Individual fish morphology and behaviour combine to influence the biomechanical performance of an animal in its environment. The interaction of fish with their dynamic and diverse aquatic environments is poorly understood, due to the complex nature of quantifying turbulence or habitat complexity. Studies show that dynamic habitats can be a hindrance (e.g. turbulent flow, Maia *et al*., 2015) or can be utilized by individuals to minimize energy use (e.g. von Karmen gait; Liao *et al*., 2003, and schooling; Li *et al*., 2020). For example, species that inhabit particularly turbulent habitats, such as rivers or tidal zones, have developed behavioural strategies that mitigate the cost by decreasing drag, hiding behind rocks, and seeking refuge in more protected areas (Liao, 2007). Likewise, in the relatively stable open ocean, schooling may offer protection from predation, but likely also helps fish economize swimming costs by utilizing the beneficial hydrodynamic forces to reduce their own energetic swimming costs (Li *et al*., 2020). Fish body form, internal and external anatomy, and behavioural repertoires have been shaped by adaptive selection in a wide variety of habitats, dictating performance and overall ecology.

### *(3) Movement Propagation Process*

Population-level movement processes are manifested by individuals (Morales *et al*., 2010). The movement propagation process underlying individual fish movement is therefore scalable and necessary to understand fish behaviour and manage fish populations. Tracking individual fish movement patterns is often summarized using several key metrics such as home range dimensions and fish network characteristics. These metrics are derived from either path data from continuous location sampling from electronic tags or detection data from discrete location sampling. The continuous sampling from satellite tags and triangulation with acoustic tags can result in path data, however, triangulation is often less precise. Acoustic tags, radio tags, and PIT tags transmit signals that have the potential to be detected by receivers at known locations thus generating time-stamped fish positions. It is with these movement data that a fish's movement propagation process can be analysed. In essence, a fish's day consists of short-term behavioural states such as swimming, feeding, and sleeping; at year or lifetime scales, fish engage in dispersal, residency, and/or migration (Dingle & Drake, 2007). As actual or estimated relocations of an individual are added over time, an individual fish's movement trajectory across a significant part of its life may be revealed and provides an opportunity to test hypotheses about movement at the species or population level and investigate the consequences of these movement patterns for competition, predation and disease risk, or conservation.

How movement tracks can be categorized and assigned to a movement class can potentially reveal the movement propagation process. We acknowledge both the probabilistic (Paris *et al*., 2013) and deterministic (Faugeras & Maury 2007) processes of movement and how both are important for understanding phases of movement. There is need for the development and incorporation of more sophisticated and realistic models of movement. There are important analytical tools available to analysts working with fish movement data to test hypotheses and calculate metrics that describe fish movement. Packages such as migrateR (Spiz *et al*., 2017) provide functionality to test hypotheses about the shape of the fish's lifetime movement trajectory. For example, Griffin *et al*. (2018) tested hypotheses about the shape of Atlantic tarpon (*Megalops atlanticus*) movements to reveal their migratory tendencies. Range-restricted movements can be analysed to calculate dimensions of a home range or core area (noting that there is growing interest in using continuous time movement models; Hanks *et al.,* 2015), which can be used to compare how individuals use space or identify overlap with key habitat types or infrastructures. Identifying home range areas can substantiate the importance of marine reserves for fish species such as queen triggerfish (*Balistes vetula*), which was found to have its home range within the marine reserve Buck Island Reef National Monument in St. Croix (Bryan *et al*., 2019). More specifically, tools such as resource selection functions and potentially step selection functions can be used to test hypotheses about how specific habitat types are used to engage in different types of behaviour (Griffin *et al*., 2021). Both resource selection and step selection functions will become more important tools for analysing fish movement propagation processes, but require continuous path data to be overlaid with reliable habitat maps, both of which can be practically challenging to acquire. At large scales, hidden Markov models (HMM) can be fit to movement paths to identify movement states and transitions between states such as resting, travelling, and foraging-like behaviour. Papastamatiou *et al*. (2018*b*) identified the diel variation of two movement states (relatively low activity and relatively high activity) in blacktip reef sharks and grey reef sharks (*Carcharhinus amblyrhynchos*) with the use of HMMs, which showed that both species had a higher activity level during night-time but with varying probability. When broader movement patterns are known but actual movement paths are not measured, statistical movement models such as random walks can be used, for example, to estimate fish home range sizes and spatial connectivity (Papastamatiou et al. 2013). At finer scales, accelerometery has been valuable for classifying behaviours and activity levels as individuals move through water. For example, Wright *et al*. (2021) assessed the timing and depth of fast starts in yellowfin tuna (*Thunnus albacares*) with the use of accelerometer sensors, with results suggesting that they attack their prey from below.

The fact that fishes live in three dimensions poses an additional challenge for observing movement. Some transmitters provide only two-dimensional positions that can dramatically misestimate habitat selection, distance travelled, speed, and co-occurrence with other tagged animals. Depth sensors in electronic tags can provide information about fish descents/ascents, including whether these movements are v-shaped or u-shaped. Hedger *et al*. (2017) found that Atlantic salmon more often followed a u-shaped pattern during their deeper descents (>200-m) as depth sensors revealed that the salmon remained close to the maximum descended depth rather than ascending soon after reaching the maximum depth. Data in the third dimension can also be used to calculate three-dimensional home ranges (Lunde, 2015), but new developments are needed to better account for depth in various other analyses such as resource selection functions for fish.

How changes in position can be interpreted as a movement propagation process is crucial to understanding fish ecology. Fundamental aspects of resource exploitation, competition with con- and hetero-specifics, predation and disease risk, energy budgeting, and vulnerability to stressors all stem from having a grasp of how and why fish move. Fish movement is predictable with models trained by movement data (e.g. Brownscombe *et al*., 2020; Vollset *et al*., 2021) and can contribute to spatial planning (Lennox *et al*., 2019a), either by predicting when fish are present/absent or using automated detection systems to inform agile decision making such as shutting down hydropower plants as migrating fish begin to arrive (Tiechert *et al*., 2020). Many of the models used for assessing the movement propagation process have been adapted from terrestrial systems where depth is immaterial, so our concepts of how to effectively include the third dimension remains somewhat limited (but see Lee *et al*., 2017 for discussion). There are also limitations with converting detection data to path data, for example, calculating home ranges from detection data at fixed stations or using position averaging (Simpfendorfer *et al*., 2002). Approaches such as position averaging are not validated to provide accurate fine-scale descriptions of fish movement.  Network analyses are a promising tool for describing fish movement propagation from pure detection data (Whoriskey *et al*., 2019). However, more work in this space is also needed to integrate information about depth and additional contexts in the data that may be usable for ascertaining positional information of fish.

## V. Population Level Processes

Moving as an individual or as a group has costs and benefits that many fish species must consider (Krause & Ruxton, 2002). Individual fish decisions reflect trade-offs in internal state and/or in social state, all under dynamic environmental conditions. Individuals need to balance biological and physiological traits, such as the need to feed or thermoregulate with the increased energetic costs of searching, and social traits, such as schooling or shoaling (not unlike schooling except coordinated movement is not required such that animals stay in one location) with conspecifics to socialise or gain antipredator benefits (Magurran, 1990). The broader context of the local environment weighs heavily on these decisions; factors like topography, salinity, turbidity, depth, light-levels, and water chemistry can either attract or deter fish from certain habitats. Individual- and group-level decision-making processes in fishes are so refined and interlinked, that individuals also rely on the behaviour of others to enhance the accuracy of their own decisions through processes such as quorum decision-making, which can guide collective decisions on where to move (Ward *et al*., 2008).

In instances where individual decisions align with other individuals, schools or shoals can form that either persist in the short, medium, or long term, or constantly divide and reform, leading to fission-fusion dynamics within the population (Couzin & Laidre, 2009). Benefits from moving together range from hydrodynamic savings and protection from predation to optimizing navigation, however, moving together also has costs. Population-level processes can be exaggerated with important implications for species distribution, ecosystem dynamics, habitat availability and species conservation, to name a few. The redistribution of large numbers of individuals in space and *en masse*, can lead to stark shifts or pulses in nutrient supply (Allgeier *et al*., 2017), changing the surrounding environment by increasing abiotic effects, in turn leading to substantial repercussions for ecosystem functioning (Benkwitt *et al*., 2021). Schooling behaviour can also influence population demographics through the generation of inter- and intraspecific interactions. Consequently, within any given population, moving together can affect reproduction through encounter rates, social interactions through greater opportunities to group with others, and the diffusion of information and/or disease through the physical structuring of individuals in space relative to one another (Pavlov & Kasumyan, 2000; Croft *et al*., 2009; Hasenjager *et al*., 2020).

Fishes are not bound by cross jurisdictional boundaries and often inhabit/move across multiple different management zones (Lédée *et al*., 2021, Huveneers *et al*., 2021). Therefore, understanding the extent and distance of movement in species, the proportion of individuals that undertake migration, and the level of social/collective behaviour within the population has important ramifications for conservation and management (Cooke *et al.,* 2022). Only with a better understanding of all of these complex, interconnected processes, often derived through tracking technologies and spatially and/or socially informed movement models, can predictions be made about the dynamics, demography, distribution, and structure of populations of ecological or conservation interest (Morales *et al*., 2010).

## VI. Ecosystem Level Processes

Throughout aquatic environments, fish movements affect the flow of energy and nutrients both directly and indirectly, and there has been a particular research focus on migratory species. Anadromous migrations of salmonids (*Oncorhynchus* and *Salmo* spp.) transport nutrients from the marine environment to freshwater ecosystems, providing foraging opportunities for a variety of consumers (Gende *et al*., 2001; Levi *et al*., 2015; Furey *et al*., 2016) and aiding riparian plants and communities via carcass deposition (Ben-David *et al*., 1998; Helfield & Naiman, 2001; Naiman *et al*., 2002; Quinn *et al*., 2018). The migrations of iteroparous potamodromous species, such as suckers (*Catostomus* spp), also provide nutrient transfers indirectly (Childress *et al*., 2014) via egg deposition and excretion (Childress & McIntyre, 2014). Similarly, out-migrations of juvenile anadromous fishes from freshwater provide foraging opportunities to consumers in coastal ecosystems. For example, through restoration of western Atlantic river herring (*Alosids* spp), there is potential to benefit the entire marine food web by reducing pressures on other forage fishes and relaxing pressures among competing consumers (Dias, Frisk & Jordaan, 2019). In tropical rivers, seasonal migrations of herbivorous fishes link eutrophic and oligotrophic systems, causing shifts in food web structure and potentially subsidizing predators (Winemiller & Jepsen, 1998). Broadly, migrations act to redistribute energy and feeding opportunities within and among landscapes, affecting consumer behavior and feeding, as well as food web structure, influencing the ecology and evolution of both migrants and predators (Sabal *et al*., 2021). In fact, migrations of prey fishes can induce large-scale movements of predators, a concept known as migratory coupling that has the potential to affect food web structure and ecosystem function (Furey *et al*., 2018).

Although larger-scale migrations are highly studied, smaller-scale movements by fishes also affect energy flow and food web structure. For example, consistent movements by snook (*Centropomus undecimalis*) led to coupling among marshes, riverine, and estuarine systems, acting as a vector for nutrient transport (Rezek *et al*., 2020). Even over tidal cycles, the movements of sharks in and out of coral reefs can induce temporary trophic cascades via non-consumptive effects on lower trophic levels (Rasher *et al*., 2017). In marine systems, spawning aggregations of camouflage grouper (*Epinephelus polyphekadion*) were targeted by sharks, leading to the maintenance of inverted trophic pyramids, with exceptionally high biomass of predators relative to prey on coral reefs (Mourier *et al*., 2016). Inverted biomass pyramids may be maintained by the movements of consumers (many being fishes), thereby providing energetic subsidies (Trebilco *et al*., 2016). Broadly, the movements of generalist consumers across habitat types can provide ecosystem stability, particularly in ecosystems characterized by strong temporal variability in resource availability (McCann, 2000; McMeans *et al*., 2015).

Further opportunities remain to understand and quantify the impacts of fish movements on the flow of nutrients and energy within food webs and among ecosystems. Examples include the value of fishes as seed dispersers (Mulder *et al*., 2021; Correa *et al*., 2015), the ability of fishes to transport nutrients from mass mortality events of terrestrial vertebrate migrants (Subalusky *et al*., 2017), the transfer of nutrients vertically within marine systems (via diel vertical migrations; e.g., Martin *et al.*, 2021), and more broadly the value of fish movements in understanding biodiversity (Jeltsch *et al*., 2013). Integrating technologies that quantify movement (such as telemetry; Cooke *et al*., 2004; Hussey *et al*., 2015) as well as other aspects of food webs (diet, stable isotopes, energetics) and communities will likely be needed to improve our understanding.

## VII. Movement Ecology Meets the Conservation and Management of Fishes

Understanding a species' movement ecology is fundamental to its effective management and for the development of effective conservation actions and policy measures (Driscoll *et al*., 2014; Barton *et al*., 2015; Allen & Singh, 2016). At a basic level, successful fisheries management is linked to knowing where and when fishes reside or migrate (Thorstad *et al*., 2013), and the integration of movement ecology with management goals supports the conservation and protection of fish habitat and populations (Crossin *et al*., 2017; Matley *et al*., 2022). There are numerous elements within the conceptual framework for movement ecology presented herein that can inform effective fisheries management or conservation by linking the focal individual to their environment, notably their movement path, capacity for motion, interaction with their environment, and internal state. All of these factors influence catchability in complex ways (Lennox *et al*., 2017). Whereas the conceptual framework by Nathan *et al*. (2008) is focused around the individual and how its movements are influenced by internal state and environmental interactions, this individual-based information can be scaled up to help with management of fish populations as a whole (Metcalfe *et al*., 2012).

Movement paths are an emergent property of an individual's capacity for motion and how they perceive and navigate through the environment. Understanding these elements is critical for identifying and protecting movement corridors and describing the environmental cues that initiate life history events like migration and allow an individual to return to their natal systems for spawning. This is well illustrated by Pacific salmon where fisheries management organizations plan their stock assessment activities around the movement paths of salmon during their coastal approach and where regulators apply regulations in different zones to manage stocks. For example, adult sockeye salmon returning to the Fraser River of British Columbia have the option of approaching from the south of Vancouver Island through Juan de Fuca Strait or diverting to the north of the island and coming south through Johnstone Strait (McKinnell *et al.*, 1999). Failure to account for differences in movement paths would reduce the validity of stock assessment and make it difficult for the development of fisheries management plans (e.g., when and where to open a fishery). The same can be said for marine fish in open-ocean environments. Going back to early work by Block *et al.* (2005), satellite telemetry has revealed unexpected population structure of bluefin tuna and thus revolutionized the management of these populations. Additional work on tuna in other environments (e.g., Teo *et al.,* 2007) has revealed similar unexpected knowledge on trans-boundary movements that is highly relevant to the governance of migratory fishes.

Inherent to an understanding of movement pathways are the biomechanics of an individual's movement that manifest as their capacity for motion. Understanding a species' ability to move dictates the size and/or distribution of habitats they may occupy. Fishes display a wide range of movement patterns from those that are largely resident within small home ranges to those that may roam throughout the world's oceans (Green *et al*., 2015). Further, migration range and movement speeds not only scale well with the size of the fish, but can be higher than expected in fishes that can retain metabolic heat (e.g., thunnids; Watanabe *et al*., 2015), reinforcing the connection between the internal state of an individual and their movements. An understanding of the timing and extent of movements (or lack thereof) for focal species is essential for defining the boundaries of conservation zones or reserves (Kramer & Chapman, 1999; Simpfendorfer *et al*., 2010), which when developed with this type of input can promote increased diversity, biomass, and density of focal species within their boundaries (e.g., Halpern, 2003; Lester *et al*., 2009). Indeed, in the Mediterranean Sea, species density was higher in protected areas that were larger than their home range, but only 25% of existing protected areas in this region were large enough to provide adequate protection for the 11 species that were assessed (Di Franco *et al*., 2018). Similarly, fisheries plans the make use of fish aggregative devices (FADs) benefit from knowledge of abilities to transit open water habitats and locate FADs (Girard *et al*., 2004). An understanding of a species' movement capacity and the resulting area they use can help during the design phase of protected area networks, and can be an important element in facilitating discussions with stakeholders and garnering buy-in for more expansive protected areas (Weeks *et al.*, 2017).

The movement capacity of a species can also inform the partitioning of fish stocks into management units or zones (Hayden *et al.*, 2017; Kessel *et al.*, 2018) and the scale and extent of a species' metapopulation (Daniels *et al.*, 2008). Inherent to the definition of a fish "stock" is the notion that individuals in the stock are largely spatially or temporally isolated from other conspecifics (Ihseen *et al.*, 1981) and thus movements within and among stocks will dictate the optimal boundaries for their management (Hourston, 1982; Binder *et al.*, 2017). This delineation is further complicated, however, when the range of a stock spans international boundaries since different management measures may be applied in each region. An exploration of movement ranges for three fishes in Lake Tanganyka, an African Great Lake, found evidence for movements by two species outside of Zambian waters and as such international-level management strategies were recommended to ensure fisheries regulations were effective (Phiri & Shirakihara, 1999). Evidence of high spawning site fidelity in walleye (*Sander vitreus*) in another transboundary system (Lake Erie) identified the need for increased focus on individual stocks, despite the fact that there was extensive mixing of stocks outside of their spawning season (Hayden *et al.*, 2017). Tagging of adult Atlantic bluefin tuna off the coast of eastern Canada revealed evidence of a metapopulation requiring more spatially explicit management than the current simple two-stock structure that had been used for some time (Galuardi *et al.*, 2010). These types of studies demonstrate how knowledge of the movement capacity of a species throughout their life history is critical for establishing appropriate management zones and facilitating international management collaboration to provide adequate stock protection.

There is considerable literature exploring the movement capacity of fishes related to their swimming mechanics and speed (e.g., Webb, 1998; Sfakiotakis *et al.*, 1999; Liao, 2007; Cano-Barbacil *et al.*, 2020). In lotic systems, this capacity for movement will dictate whether an individual is able to move upstream to complete their life history in natural systems or those with modified flow regimes or barriers that can impede connectivity (Williams *et al.*, 2012). This type of information has been used to revise the timing and magnitude of alterations to discharge in regulated rivers, which can help limit impacts on fishes living downstream (Göthe *et al.*, 2018).

Additionally, movement capacity has been used to inform the effective design of structures at instream barriers to allow passage to critical foraging or spawning grounds in an effort to maintain or restore connectivity (Castro-Santos & Haro, 2005; Silva *et al*., 2018). For example, anguillids move upstream to reach productive rearing habitats and passage of barriers must be facilitated. Passage structures with appropriate substrata and suitable slopes are therefore being designed based on the climbing abilities of juvenile (glass) eels (Jellyman *et al*., 2017; Watz *et al*., 2019). These types of barriers can also pose hazards for fishes as they move downstream (Williams *et al*., 2012), and another element within the conceptual framework, cognition, can be used to shift a fish's movement path away from hazards and towards areas of safe passage. Various behavioural guidance strategies involving light, carbon dioxide, louvers, bubble curtains and noise have been used with variable success to repel fish from undesirable areas and/or attract them to desirable areas (reviewed in Noatch & Suski, 2012). An understanding of the movement ecology of lotic fishes is clearly essential for limiting impacts from changes in discharge and barriers to both upstream and downstream migration.

The internal state of an individual drives movements to support foraging, reproduction, and maintenance of homeostasis. For managers, this is presumed to manifest as movements towards habitat that can meet these internal demands, or the absence of movement (i.e., residence) within suitable habitat. Understanding the key habitat parameters, whether biological (e.g., sufficient prey resources), limnological (e.g., optimal temperatures for maximum growth), or physical (e.g., suitable substrate for spawning) that may push, pull, or retain fishes is key for effective management of habitat. In addition to inclusion of important habitat in protected areas (Green *et al*., 2015), understanding habitat requirements is also critical for effective habitat creation or remediation (Lapointe *et al*., 2013). When implemented successfully, such activities can promote recovery of fish populations, but when the needs of individual fish are not being met, habitat interventions can at best fail to yield improvements and at worst, result in the creation of population sinks.

## VIII. The Future of Fish Movement Ecology- Unknowns and Opportunities

Evidence syntheses (such as what we have provided here) are useful for identifying research gaps.  We have done so here but also note that there is an intimate connection between the tools available to study fishes on the move and the questions that we can answer. Here we briefly outline the future of fish movement ecology by addressing both technological innovations (of today and on the horizon) and their role in addressing knowledge gaps. Our goal was not to list every possible research need or opportunity related to fish movement given that has recently been covered by Lennox *et al.* (2019b).

Fish movement ecology research will continue to develop in extreme directions - longer lifetime tracking, finer resolution of observations, smaller electronic tags to better understand larval and juvenile fish, and better sensor integration (e.g., environmental sensors, accelerometers to quantify movement behaviour, heart rate sensors to quantify costs of movement) to reveal novel insights into the internal and external drivers of movement (Lennox *et al.,* 2017; Matley *et al*., 2022). Positioning systems are increasingly being used to reveal three-dimensional positions of fish, allowing fine grained matching of positions to resources such as physical habitat (Griffin *et al*., 2021) or classification of behavioural states (Whoriskey *et al*., In Review). These positioning tools tend to be limited to smaller closed areas such as ponds, lakes, or embayments, but large lakes are increasingly gridded with receivers (e.g., the Laurentian Great Lakes, see https://glatos.glos.us/) and may soon have the capacity for high dimensional long-term positioning of fish to reveal drivers of large-scale movements (Lennox *et al*., 2021*a*). Laboratory tools for tracking individual fish by video provides new and robust tools for movement experiments and are suitable for larval life stages (e.g. TRex tracking; Walter & Couzin, 2021). Miniaturization of transmitters on high frequency channels is opening new opportunities for field investigations of fish larvae (Martinez *et al*., 2021) including a tag weighing only 0.08 g in air (Deng *et al*., 2021). Beyond fine-scale movements, satellite tags continue to improve and provide scientists with the ability to track animals over broad spatial scales (Harcourt *et al.,* 2019; Sequeira *et al.,* 2019). Like other electronic tags, satellite tags continue to shrink in size such that they can be applied to a broader range of species and life stages and provide tracks with greater resolution and accuracy.

Larger tags that transmit sensor data in addition to individual ID are increasingly used to reveal more about the ecology of fish movement using telemetry. Depth and temperature sensors are commonly integrated into both transmitting and logging tags to add context to where, when, and why fish move. Conductivity (salinity) sensor tags are also available for externally attached tags and oxygen sensor tags have been tested, although both sensors have short longevity due to biofouling of the sensors. Studies on individual costs and benefits of movement benefit from integrated acceleration, heart rate, or even blood metabolite sensors that log the data or transmit to receivers. Heart rate loggers are increasingly used (e.g. Twardek *et al*., 2021) whereas radio transmitters equipped with heart rate sensors have been used for decades (Lucas, 1994). Magnetometers have the potential to reveal new insights about fish navigation at finer scales than have ever before been possible using turning angles from path data. Predation sensor tags are also available to resolve the fate of fish and efficiently exclude observations from non-target species (Klinard and Matley, 2020; Lennox *et al*., 2021*b*). Temperature sensors have creatively been applied to monitor gut heat of tunas to identify foraging areas (Whitlock *et al*., 2013) and to reveal predation by endothermic animals (Wahlberg *et al*., 2014), which could also be used to identify behavioural fever in response to pathogens or stress (Huntingford *et al*., 2020). Of course, it is also possible to measure biomarkers (e.g., omics, isotopic signatures, genetics, endocrine state) on fish that are tagged and released (or recaptured) to also generate understanding about the drivers and consequences of behaviours (see Brosset et al. 2021 and Thorstensen et al. 2022 for reviews).

There are still challenges modelling the vast data recovered from telemetry systems (Nathan *et al*., 2022). Programs for synchronizing receiver clocks and calculating three-dimensional positions such as YAPS (Baktoft *et al*., 2017) can take months of computing time to parse through a large dataset. Modelling both detection data and path data (i.e. after triangulation) must use models that account for the high degree of spatial and temporal autocorrelation in the data, including home range calculation (Signer & Fieberg, 2021) and generalized linear models (Whoriskey *et al*., 2019). Development of efficient model fitting tools is needed if the massive datasets accumulating from telemetry platforms are to be analysed effectively. Tools for developing and accessing fine scale environmental data are also needed to relate fish movement to external drivers (i.e. menotaxis; Togunov *et al*., 2021). Large parts of the ocean are not mapped and satellite measures of sea surface temperature, wave height, tidal phase, wind direction, current velocity, salinity, and chlorophyll - at an increasingly fine-scale resolution - should be easier to access and match to movement data to develop models of animal range and resource selection based on occurrence or movement data (Griffin *et al*., 2021). In fact, there are an increasing number of studies that use ocean remote sensing to develop models of resource selection by fish at regional, ocean-basin and global scales thanks to advances in biotelemetry and environmental monitoring (El Mahrad *et al.,* 2020). Additional contextual information for tagged animals about the biotic environment are also needed, including details about local conspecifics, competitors, and predators that are presently difficult to resolve without cameras or use of VMT devices (e.g., Barkley *et al.,* 2020). However, such contextual information can obscure some important drivers of movement and can especially complicate investigations of sociality or symbiosis in fish if they are interacting with both tagged and untagged counterparts.

Novel tools and techniques for magnifying animal movement and generating better, finer resolution observations of individual locations and paths that will allow more robust testing of hypotheses about the individual- and group-level internal and external drivers of movement are emerging (e.g. Monk *et al*., 2021). Both observation-based and automated classification of behavioural states from movement data will become easier and more efficiently linked to habitats to identify activity and behavioural landscapes where fish partition their energy (Brownscombe *et al*., 2017), and struggle to survive and reproduce in a challenging and changing world (Monk *et al*., 2021). Indeed, fish movement ecology must strive to begin unravelling how and why fish distributions are changing with climate change and responding to increasingly intense human exploitation of the ocean, as well as provide insights into the drivers of fish extinction and extirpation as the biodiversity crisis continues to worsen.

## IX. Conclusion

Movement is a ubiquitous feature for fishes. Although the scale and reason for such movements can vary, it is clear that movement is fundamental to the ecology and life-history of fish populations. Recent technical innovations (e.g., electronic tags, hydroacoustics, chemical tracers) have enhanced our ability to study the movement ecology of fishes in the wild and in doing so have revealed immense diversity in how fish move through aquascapes, whether in small freshwater streams or the high seas. The movement ecology paradigm proposed by Nathan *et al*. (2008) provides a framework for understanding the basis for the diversity in movements and understanding environmental- and individual-level drivers. Given the manifold effects of water temperature on fishes (i.e., being ectotherms; Fry, 1971), the environment has a strong influence on all aspects of movement (e.g., from controlling muscle enzymes that enable locomotion to regulating respiration to enabling maturation), which led us to make some minor modifications to how the framework is conceptualized (see Fig. 1), though it is clear that the conceptual basis for the framework is sound and highly applicable to fishes. There is existing and emerging research on all aspects of the framework but we note that the greatest focus to date has been on the effect of environmental factors on movement – a similar observation made by Joo et al. (2022) in a review of how the Nathan et al. (2008) framework had been applied across taxa.  We further extended our review of movement ecology to consider higher level processes, such as what movement means for fish population biology, community interactions, and ecosystem function. Given the importance of movement for ecology and evolution, we also considered what the movement ecology of fish means for management and conservation. There are a growing number of applications that span various domains of the movement ecology framework, which are providing fisheries managers with new tools and knowledge for protecting, restoring, and managing fish populations (Cooke *et al.,* 2022). Yet, there remains many unknowns about the fundamentals of fish movement ecology, including the generality of various physiological phenomena and how different aspects of movement may be influenced by climate change (see Lennox et al. 2019a for research agenda). It is not an exaggeration to suggest we are entering the golden age of fish movement ecology, representing an exciting time to be a fish ecologist.

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## XI. Data Availability Statement

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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