

Applied aspects of locomotion and biomechanics

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Locomotion is the act and process of moving from place to place, which is fundamental to the life history of all mobile organisms. While the field of biomechanics encompasses the study of the physical constraints of what animals are capable of, ecological contexts require an integrated view that includes ecology and behavior. This chapter provides an overview of some of the areas where locomotion and biomechanics of fish movement interface with the rapidly evolving changes that humans impose on aquatic

environments. These changes include fundamental alterations to the environment such as altered flows, fragmentation of riverine habitats, and invasive species, but also direct interactions that occur with capture fisheries. We explore each of these areas, considering both challenges and opportunities informed by the study of locomotion and biomechanics, emphasizing how this field can contribute to conservation of fishes in the Anthropocene. We then turn to technology, where important advances are aiding in our understanding of fish movement. In some cases those advances have themselves led to novel technologies, where biomimetic robots and related devices offer novel opportunities, both for conservation and for other pursuits.

1 Introduction

The study of fish locomotion and biomechanics presents humans with challenges and opportunities as we navigate the Anthropocene.^a These challenges include recognizing and mitigating anthropogenic influences such as habitat quality, quantity, and access, and developing sustainable approaches to harvest fisheries. At the same time, technological advances have enabled humans to better understand the mechanics of aquatic locomotion, providing both challenges and opportunities for conservation and engineering. We begin this chapter with a broad overview of fish swimming and biomechanics, identifying both physiological and behavioral constraints that are particularly relevant to management and conservation. We then describe some challenges confronting fisheries managers and how they relate to locomotion, paying particular attention to topics of habitat fragmentation, invasive species, and harvest fisheries. We conclude with a brief review of recent advances in biomimetic engineering that may offer opportunities for developing sustainable approaches to harvest fisheries and for informing the design of swimming machines and other devices, which may themselves open opportunities for exploration and greater understanding of the world in which we live (Fig. 1).

The way fish move through their environment has captured the imagination of researchers since at least the time of Aristotle (350 BCE) (Aristotle, 1937). To propel themselves through water, fish must exert a force against a medium that deforms continuously. This is in marked contrast to propulsion on land where animals can push off a solid surface to move about. The ability of fishes to move through the dense and viscous aquatic medium with such apparent ease has been influential in stimulating both theory and experiments in the field of fluid mechanics and hydrodynamics of fish locomotion (Alexander, 1983; Lighthill, 1960, 1975; Vogel, 1981).

Fish achieve effective propulsion through a variety of mechanisms, with the unifying characteristic of establishing pressure gradients along their fins and/or

^aAnthropocene is a term used by scientists and nonscientists to highlight the concept that we are living in a time when human activities have significant effects on the global environment. The Anthropocene currently has no formal status in the Divisions of Geologic Time and is not recognized by the USGS. Use of this term is informal.

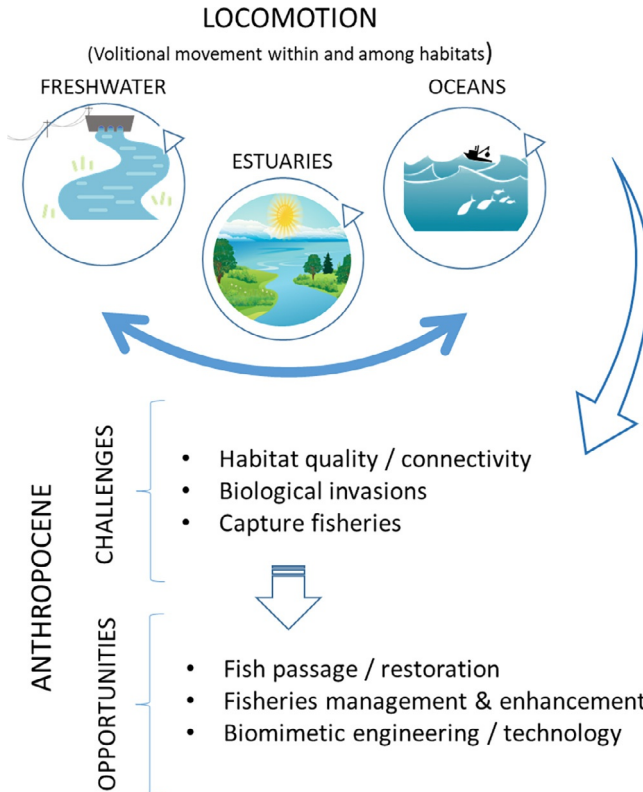


FIG. 1 Conceptual relationships among movement, habitats, challenges, and opportunities associated with the study of locomotion and biomechanics.

bodies, generating force on the surrounding fluid that determines their path of motion. The amount of thrust produced and the efficiency of force transmission is largely driven by body and fin morphology, coupled with skin, skeletal structure, muscular design, and composition (Shadwick and Gemballa, 2006). Most species of fishes move primarily using their body and caudal fins (BCF) for propulsion, while median and paired fins contribute greatly to body stability and maneuvering during locomotion. Body undulation generates thrust through a propulsive wave propagating along the body, which is characterized by wave speed, wavelength, and amplitude of the lateral oscillation (Fig. 2).

The habitats occupied by fishes are hugely diverse, ranging in scale from pan-global marine environments traversed by species like tunas and lamnid sharks (Block, 2005; Block et al., 2001), to the interstitial spaces between the gills of host species and other tiny spaces (Breault, 1991). This diversity of habitats has led to a correspondingly dramatic diversity in both morphology and swimming performance. In some cases, it may be possible to make general predictions about the habitat a fish occupies and its ability to negotiate

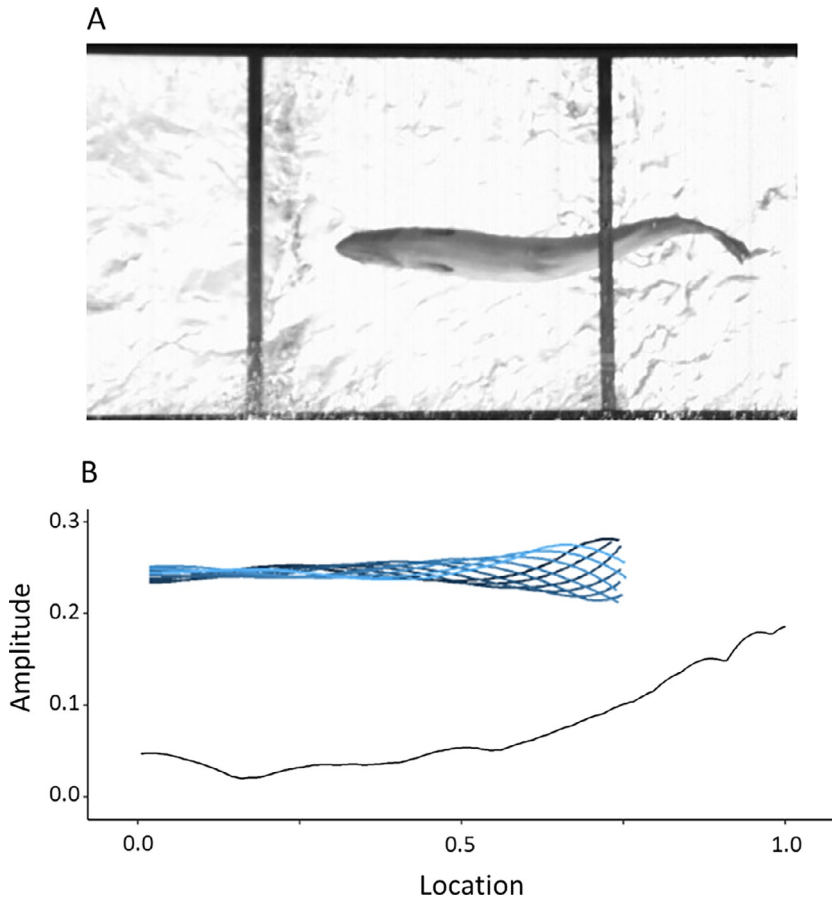


FIG. 2 (A) Atlantic salmon swimming at 10 body lengths per second ($BL\ s^{-1}$) in an open flume. (B) Digitized midlines for one tailbeat (overlaid curves, ranging from blue (start of stride) to black (end of stride)), and associated maximum lateral amplitude along the body, presented as proportion of the body length from location 0 (head) to 1 (tail).

certain environments, simply by viewing its external morphology (Webb, 1984, 2006). At the same time, though, diverse adaptations may be constrained by similar physical principles, leading to a surprising level of convergence in kinematics across taxa when fish are performing similar tasks (Di Santo et al., 2021).

There are exceptions to these patterns of diversification and convergence, however. Some fish species have developed morphologies and behaviors that allow them to interact with solid structures within their environments in ways that promote movement or allow them to maintain position, e.g., by attaching to a substrate or a host animal (examples include parasitic lamprey

(*Petromyzon* spp.; Beamish, 1980), remoras (family Echeneidae; Wang et al., 2017), and many benthic species (Webb, 1984, 1989), which use the substrate to escape rapid free-stream flows). Both the general patterns and these exceptions have important implications for how humans and fish will interact during the Anthropocene.

While essential for understanding the mechanics of locomotion, movement itself is not governed solely by external morphology and biomechanics. Other aspects, such as internal structure and physiology, are equally relevant, including vascular circulation (Farrell and Steffensen, 1987), aerobic capacity (Brett, 1964), and the distribution and abundance of aerobic and anaerobic muscle fibers (Jayne and Lauder, 1994; Rome, 1994).

The distribution and abundance of aerobic and anaerobic musculature has important implications for locomotion, and for ecology in general. Fish species that specialize in fast starts and sprinting tend to have proportionally greater amounts of anaerobic muscle, while those that specialize in cruising have more aerobic muscle (McLaughlin and Kramer, 1991). More aerobic muscle requires greater blood flow and overall greater aerobic capacity, which in turn allows those species to sustain greater swim speeds. Moreover, the high metabolic demand of aerobic tissues can necessitate greater activity to ensure sufficient resources are gathered to meet these demands (Brett and Groves, 1979; Ware, 1975, 1980). Provided that sufficient oxygen and nutrients are available to the fish, aerobically fueled swimming can be sustained indefinitely. As we will see below, this has important implications for conservation and management. When fish exceed their maximum sustained swim speed (U_{ms} ; Table 1) they begin to recruit anaerobic metabolic pathways and switch to using the generally more abundant white muscle fibers. This is usually done incrementally, allowing fish to prolong their endurance by interspersing bouts of anaerobic swimming with aerobic swimming (Brett, 1964; Peake and Farrell, 2004; Rome et al., 1992a). Thus, “prolonged” swimming describes a narrow band of speeds at which both processes are important in producing thrust. However, as speeds increase further the fish enters “sprint” mode. Sometimes described as “burst” mode, this is powered almost entirely by anaerobic processes and can be sustained only very briefly (the actual limits vary by species, but 20s is a commonly described threshold; Brett, 1964).

The existence of these three modes: “sustained,” “prolonged,” and “sprint” has been documented for a wide variety of species (Beamish, 1978). Importantly, species that have greater aerobic capacity do not necessarily have greater sprinting ability (Clark et al., 2013). This can be an important factor limiting access to habitats: assumptions that less active species will be less able to traverse barriers may be inaccurate, with potential consequences for management.

Our understanding of swimming modes is influenced by the methods used to measure and describe them. Maximum sustained speeds (U_{ms}) are

TABLE 1 Definitions, metrics, and indices describing fish locomotion—the act and processes associated with moving from place to place, such as swimming, jumping, walking, etc.

Term	Definition, metrics, and indices		Units
Ability	Also Capability or Capacity: the physical and physiological bounds describing the limits of what an organism is capable		
	Endurance	Time to fatigue (T) while executing a given task such as swimming at a constant speed (U_s), described by the relation $\ln(T) = a + bU_s$	s or min U_s , a , and b
	Speed	<ul style="list-style-type: none"> Maximum sustainable swim speed (U_{ms}) Maximum speed sustained for a fixed interval without fatigue, typically 20–200 min (U_{crit}) Maximum attainable swim speed (U_{max}) 	$BL s^{-1}$ or $m s^{-1}$
	Acceleration	<ul style="list-style-type: none"> Maximum acceleration (A_{burst})^a 	$BL s^{-2}$ or $m s^{-2}$
Performance	The effective execution of a task (e.g., traversing a velocity challenge, avoiding capture, or accessing refuge)		
	Distance/ Height	Maximum distance traveled (D_{max})	BL or m
	Success	Probability of success	Success attempt ⁻¹ Success h^{-1}
Motivation	The inclination or willingness to perform a task (e.g., move)		
	Attempt rate	Number of attempts per time period or proportion of a population staging attempts per unit time	Attempts h^{-1} $P(\text{Attempts}) h^{-1}$
	Effort	The amount of effort expended to achieve a task	$\%T U_s$ $\% U_{msr} U_{crit}$ U_{max} , or A_{burst}

^aNote that U_{burst} is a term that is often used to describe either fast start or sprint speeds (and even in some cases prolonged speeds). We distinguish it here, as sprint and prolonged speeds are defined by endurance relationships and cannot be represented by a single value.

frequently estimated using a process whereby fish are confined within a chamber or tunnel and subjected to flow speeds that increment steadily on a fixed time interval (Brett, 1964). The speed at which fatigue begins to occur within that time interval is hindcast and recorded as the “critical swim speed” (U_{crit}). When the time interval for each velocity increment is sufficiently long (e.g., ~ 200 min) U_{crit} serves as an estimate of U_{ms} . This technique is excruciatingly slow, however, prompting most researchers to greatly shorten the time intervals. A key consequence of this is that U_{crit} becomes unreliable as an estimate of U_{ms} and may be biased by accumulation of anaerobic byproducts during intervals that preceded the fatigue event (Hammer, 1995; Lee et al., 2003). Prolonged (generally thought of as speeds $> U_{ms}$ that can be sustained for $> \sim 20$ s) and sprint speeds (those that result in fatigue in $< \sim 20$ s) are typically estimated by rapidly increasing flow velocity to a desired test condition and then holding that value constant until the fish fatigues. The relation between flow velocity and endurance characterizes each of these modes.

One consequence of conducting these tests within confined chambers is that fish tend to fatigue at speeds considerably lower than what occurs in more natural settings (Castro-Santos et al., 2013; Tudorache et al., 2007, 2010). Tests performed in larger channels and using volitional swimming against high velocity flows have shown that many species of fish are capable of swimming at speeds nearly double what previous studies had predicted, suggesting that estimates of performance from the literature should be viewed with skepticism (Castro-Santos, 2005; Castro-Santos et al., 2013).

1.1 Temperature and locomotion

Another important distinction between aerobic- and anaerobic-powered locomotion is the importance of temperature. Fish species occupy habitats with temperatures ranging from $< 0^\circ\text{C}$ to $> 44^\circ\text{C}$ (Bargelloni et al., 1994; Kock, 2005; Lozano-Vilano and De La Maza-Benignos, 2017; Minckley and Minckley, 1986). Most fish are ectotherms, and their metabolic rates vary predictably with temperature. At low temperatures, the scope for activity is reduced and fish tend to be less active. Both basal metabolic rate and scope increase with temperature; however, as temperatures exceed a certain critical value the costs of maintenance increase, and scope declines. Hence, reduced activity is common among fish exposed to temperatures that fall above or below their thermal optima (Brett and Glass, 1973; Brett and Groves, 1979).

The effect of temperature on aerobic swim speeds is much greater than it is on anaerobic speeds. In both cases, chemical reactions occur more rapidly at warmer temperatures. This means that the rates of nutrient delivery, waste removal, and rate of ATP production all increase, raising the potential for power production, as well as the maximum contraction speeds of both red and white muscles (Rome et al., 1992a,b; Wardle, 1975). The benefits of increasing temperature change when thermal optima are exceeded, however:

as temperatures continue to increase, so do maintenance metabolic costs (the actual mechanisms and their relative importance remain a topic of some dispute: [Clarke and Fraser, 2004](#)), and these costs add to costs of circulation, etc., which in turn places a greater proportional demand on aerobic scope. This is further aggravated by the fact that at higher temperatures the ability of water to carry oxygen and carbon dioxide diminishes, reducing the efficiency of gas transfer at the tissues and gills. At an upper critical limit, these costs exceed the ability to maintain homeostasis. Thus at both high and low temperatures, the ability to sustain aerobic swimming is compromised, and fish switch to swimming using anaerobic muscle fibers ([Pörtner et al., 2017](#)).

The reasons for this transition are not entirely clear, although some explanations appear likely. For one, anaerobic muscles use locally stored glycogen to fuel ATP production and are therefore less dependent on the circulatory system. Furthermore, the number of temperature-dependent reactions required to produce ATP are reduced compared with aerobic metabolism, and with fewer steps in the “supply chain” the overall effect of temperature on muscle kinematics is reduced ([Clarke and Fraser, 2004](#)).

These and other factors contribute to a widely observed phenomenon, whereby sustained swimming capacity is strongly influenced by temperature, while sprinting is less so ([Haro et al., 2004](#)). An important caveat to this is that recovery between bouts of sprinting does require aerobic processes, and the time required to recover between sprinting bouts is also strongly influenced by temperature ([Bayse et al., 2019](#); [Goerig and Castro-Santos, 2017](#); [Kieffer et al., 1994](#); [Wilkie et al., 1997](#)).

This does not mean that anaerobic swimming is unaffected by temperature, however. Fish commonly become sluggish, inactive or “semi-torpid” when the water temperature is near the lower end of their limits ([He, 2003](#); [Lagardère and Sureau, 1989](#); [Woodhead, 1964](#)). Temperature may also affect the startle response and reaction to predators, fishing gear, etc. Muscle kinetics are also affected, particularly at very cold temperatures: [Özbilgin and Wardle \(2002\)](#) found that the escape reflex of Haddock (*Melanogrammus aeglefinus*) in the North Sea was much lower at 7°C compared with that at 12°C, and attributed this change to reduced contraction speeds of white muscle at colder temperatures. Other studies have indicated that this pattern is widespread ([Wardle, 1980](#); [Yanase et al., 2007](#)). Given the ongoing and anticipated changes in temperatures during the Anthropocene further study of the effects of temperature on swimming capacity will be useful for informing management decisions, with important implications for conservation and effectiveness of fishing gears.

1.2 Ability vs performance

Taken together, morphology and physiology determine the limits of “capacity” ([Beamish, 1978](#)), or what a given individual fish is capable of

doing within its environment (Table 1). And the environmental context matters: metabolic rate and aerobic scope are strongly dependent on temperature; efficiency of force transmission will vary with turbulence; buoyancy is affected by depth, etc.

Importantly, though, ability is not synonymous with performance (Table 1). Performance refers to how well an animal is able to achieve a certain task, and again, each task is context dependent. For example, ability to escape an ambush predator may be governed by acceleration, maneuverability, and maximum speed, while traversing a velocity barrier or escape from pursuit or a fishing trawl may be governed by endurance or maximum sustained speeds. If fish consistently optimize the application of their capabilities to each discrete task with which they are confronted, then capacity and performance would be equivalent, but this is not the case. Instead, an animal in its environment must respond to multiple sensory inputs, its perception of risk, its internal state (e.g., nutritional or reproductive status), and other factors, many of which remain poorly understood.

Each of the issues reviewed above has relevance to various aspects of conservation and management of fishes and fisheries and also to the opportunities afforded to human engineers by improved understanding of principles, constraints, and applications. Throughout, we do not limit our content to the physiology of locomotion. Instead, we cast locomotion and movement in their environmental and applied context, explicitly recognizing that these contexts require that behavior not be decoupled from physiology. We therefore take a holistic approach, integrating behavior and physiology, as occurs in nature.

2 Habitat quality and connectivity

2.1 Syndromes of the anthropocene

Access to adequate habitat is a fundamental metric of habitat quality and is an essential requirement for healthy fish populations. Fish need to access suitable habitats to complete the various stages of their life cycle (Schlosser, 1991). Many factors may partially or completely impede fish movements, as well as the distribution of suitable aquatic habitats. Some of these factors are governed by physical attributes of the environments and locomotor capacity of fishes, while others are linked to fish behavior and ecology.

Although this volume focuses on developments and projections of the period beginning in the mid-20th Century, fundamental changes to aquatic environments from anthropogenic activities long predate this (Hall et al., 2011, 2012). Since 1950, however, fluvial and marine ecosystems have undergone accelerated changes resulting from human activities. Anthropogenic features now pervade many landscapes worldwide, altering aquatic habitat quality and connectivity. Global climate change is also modifying natural processes and physical characteristics of both freshwater and marine environments.

The multiple facets of anthropogenic influences have been synthesized under the term “syndromes” (Meybeck, 2003), which are not specific to a few areas, but instead can be observed in many places around the globe. Each syndrome has its own causes and symptoms, although there can be substantial overlap between them. Below we examine some of these syndromes and how they relate to the ability of fish to move through their environment.

2.1.1 *Instability in physical properties of aquatic habitats*

Global changes in the Earth’s climate due to human activities is currently leading to increased temperatures in most aquatic habitats, along with a reduction in pH and an increase of hypoxic zones, especially in coastal waters where organic matter and nutrients coming from runoff processes are present. Many physiological processes in fish (e.g., growth, metabolic rate, locomotor performance) are temperature- and oxygen-dependent. As a result of species’ different physiological tolerances and capacity for adaptation, a modification to the thermal regime will affect overall species distribution. Changes in water temperature may also influence fish behavior, influencing motivation to swim (Bayse et al., 2019; Goerig and Castro-Santos, 2017), triggering migrations (Otero et al., 2014), and altering attack rate during feeding events (Domenici et al., 2019). Changes in the physical properties of aquatic environments are thus likely to affect ecological processes, changing distribution of functional habitats in time and space, and affecting the fish locomotor and sensory/neural systems (Domenici et al., 2019). In addition to the thermal effects on swimming ability and energetics described above, human infrastructures can create novel opportunities for predation, creating barriers to movement and affecting population dynamics (Agostinho et al., 2012; Alcott et al., 2020, 2021).

Changes in the physical properties of aquatic habitats are also often associated with increased instability. In the marine environment, warming temperatures may cause a reduction in ocean ice and a modification in the ocean global circulation (Macdonald and Wunsch, 1996; Maximenko et al., 2013), slowing down some currents and the redistribution of heat around the globe. Resulting thermal barriers may be impenetrable for migratory fish (Otero et al., 2014; Stich et al., 2015), and alteration in the ocean’s global circulation may limit distribution of fish larvae that take advantage of ocean currents for transportation (Kettle and Haines, 2006; Smith, 2012).

Altered thermal regimes in rivers coincide with occasional droughts and associated heat waves, where rivers and lakes experience unusually low flow or elevated water temperatures and reduced dissolved oxygen levels. This may create unsuitable areas for fish (too shallow, too warm, too hypoxic, etc.) and cause previously stable habitats to become more variable or intermittent (Meybeck, 2003). This influences bioenergetics and can affect fitness (Friedland et al., 1998, 2005; Lennox et al., 2018). The survival of fish populations in these areas is then dependent on the existence of refuge habitats (deep pools, cold groundwater seepages, colder tributaries) and

the ability of fish to access them (Ebersole et al., 2020; Vander Vorste et al., 2020). This ability relates to the species locomotor behavior and ability, but also to the degree of fluvial heterogeneity and connectivity in the watershed (Dugdale et al., 2015; Dzara et al., 2019). Access to these critical refuge habitats (e.g., those necessary for short-term survival) can be as important as access to spawning or breeding habitats for population viability (Schlosser, 1991; Sedell et al., 1990).

2.1.2 *Altered flow regimes in rivers*

Large or frequent modifications in river flow are a common feature of the Anthropocene epoch; almost two-thirds of world's large rivers are regulated in order to produce energy, control floods, or collect water for human consumption or irrigation purposes, leading to temporal fluctuations and reduction in river flow (Grill et al., 2019). Fluctuations in flow caused by pumped storage facilities and hydropower plants often have a repetitive temporal component, the magnitude and frequency of which both influence aquatic ecosystems. Water collection or diversion for irrigation may affect the flow in a more stable way: a flow reduction of 50% or more leads to "neorheism," where the river will partially or completely dry up, causing disconnections of the main channel from its delta or tributaries (Meybeck, 2003), making it impossible for fish to move within the river system.

Both short-term fluctuations and reductions in flow affect aquatic ecosystems and organisms living within them. Dams and fluctuations in discharge influence sediment processes (erosion, transport, deposition) and temperature regime, causing instability or chronic alterations to the physical properties of aquatic habitats and their morphology (Capra et al., 2017). As a consequence, specific habitats such as deep pools, sand or gravel bars, oxbow lakes, etc. may become temporarily or permanently inaccessible, leading to a decrease in heterogeneity of the riverscape (Agostinho et al., 2004; Freeman et al., 2001). A reduction in river discharge may also create zones of difficult passage such as shallow rapids and riffles, and impassable falls.

These alterations in flow regimes cause substantial changes to the mosaic of riverine functional habitats (spawning, breeding, refuge, etc.), potentially requiring species to move over longer distances to find adequate habitat. Depending on the frequency and magnitude of the fluctuations, fish may have to quickly modify their habitat selection, adapting to new features or relocating to suboptimal habitats, with associated effects on fitness (Capra et al., 2017). Species and individuals with a higher inclination to move and greater locomotor ability may exhibit higher resilience in hydropeaking rivers, creating traits-based selection in fish populations (Van Looy et al., 2019).

2.1.3 *Fragmentation of riverine habitats*

Although some river systems are naturally fragmented by features such as waterfalls, rapids, or beaver dams, anthropogenic obstructions are now widely

present in many watersheds. Dams and associated reservoirs built for irrigation, flood control, or energy production purposes are some of the greatest changes affecting river systems in the Anthropocene. Although dams existed well before the beginning of this epoch (Hall et al., 2011, 2012), the rate of construction of large dams peaked between 1960 and 70 and continues apace today. The International Commission on Large Dams (ICOLD) and the Global Georeferenced Database of Dams (GOODD database; Mulligan et al., 2020) reported 58,000 large dams worldwide in 2020, with a total storage capacity of 7000–8300 km³, roughly one-sixth of the total annual discharge of all the world's rivers. However, smaller impoundments are even more widespread, numbering nearly 16 million, and with another 8000 km³ of combined storage capacity (Lehner et al., 2011).

Dams are not the only kind of human-made obstruction in river systems, however. Tide gates and dykes often restrict connectivity between estuarine and freshwater environments (Alcott et al., 2021; Rillahan et al., 2021), and the prevalence of these structures is expected to increase dramatically as nations seek to protect critical infrastructure from rising seas in a context of global climate change (De Vaate et al., 2003; Vincik, 2013; Wright et al., 2016).

Even more prevalent are road-stream crossings, the vast majority of which use culverts to pass flow. The Anthropocene has seen tremendous growth in road construction worldwide: in the United States alone there are more than 6.5 million road-stream crossings (Wieferich, 2022), most of which are believed to pose partial or complete barriers to migration. This pattern is also evident elsewhere, including in developing countries (Makrakis et al., 2012), and is probably the single greatest threat to habitat connectivity in riverine systems worldwide (Grill et al., 2019; Park et al., 2008).

Anthropogenic river features such as dams, tide gates, and culverts have the potential to delay fish movement rates in both the upstream and downstream direction (Alcott et al., 2021; Goerig et al., 2016; Nyqvist et al., 2016) and create partial or complete barriers to fish movements for various reasons: physical obstructions (e.g., a dam), disconnection in the channel continuity (e.g., a perched culvert), or hydraulic conditions exceeding the fish swimming abilities. This restricts access to complementary and/or critical habitats (e.g., spawning, breeding, or refuge habitats) for fish species and may lead to adverse consequences on individual fitness, and ultimately on population health and survival (Dudgeon, 2011; Fuller et al., 2015). Fragmentation of riverine habitats can also confer benefits, for example, by reducing rates of colonization by exotic invasive species (Zielinski et al., 2019).

2.2 Fish passage: Restoring connectivity of riverine systems

To mitigate the effects of dams, culverts, and other barriers, various engineering solutions have been developed. Culverts are usually made of metal,

concrete, or plastic pipes, which are often narrower and smoother than the natural stream channel. This creates a constriction in the flow at the inlet and the development of high velocities within the structure, which in turn may cause erosion at the downstream outlet resulting in a “perched” culvert, with the downstream end suspended above the streambed. The disconnection in the channel continuity and excessive water velocities inside the culverts are the two main causes of impeded fish movements. Fish passage through culverts may be improved either by improving design or by retrofitting with structures tailored to the behavior and ability of target species (Duguay et al., 2018b; Park et al., 2008). If resources are available, methods that require less modification of the streambed are favored, such as creation of a stream-simulation culvert (Barnard et al., 2015; Gillespie et al., 2014) or replacement by a bridge. However, the design or retrofitting of culverts remains the most common option due to a lower cost. This may include proper sizing and embedding of the culvert to reduce the slope and the degree of flow constriction, as well as the inclusion of corrugations or baffles in the structure to increase bottom roughness and hence slow down water velocities and increase hydraulic heterogeneity (Duguay et al., 2018b; Feurich et al., 2012; Hotchkiss and Frei, 2007; Wang and Chanson, 2018).

Dams, regardless of their function, generally pose impassable barriers to most riverine fishes. The most drastic way to restore access to fluvial habitats fragmented by dams is to remove the dams themselves. In some contexts, such as aging dams constructed for mill operation or obsolete flow regulation purposes, this is the most logical option. There is currently significant interest in dam removal, frequently requiring extensive design and planning (including the restoration of riverine geomorphic processes (Bellmore et al., 2019; Ryan Bellmore et al., 2017; Wiefelich et al., 2021)). Dam removal often has positive effects on fish access to habitat (Hill et al., 2019; Hogg et al., 2015; Magilligan et al., 2016), however, there can also be less desirable consequences, for example, by favoring access to new habitat for invasive species (McLaughlin et al., 2013; Stanley and Doyle, 2003). Sometimes the original structures were placed at falls or similar barriers to movement: in such cases removal may have negligible benefits for providing access; likewise, the surrounding riverscape may have been so altered by the construction and operation of the dam that simple removal fails to restore connectivity.

The dam removal movement coincides with countervailing demands to increase hydropower production to replace fossil fuels. Thus, in many cases dams are likely to persist despite their consequences on fish movements and access to habitat, elevating the need for effective mitigating solutions. Fishways are structures designed to provide a passage route, usually around a dam or similar structure but are sometimes used to provide access past natural barriers as well (Hatry et al., 2013). Although fishways are used to pass fish in both upstream and downstream directions, the challenges and risks associated with the two types differ, leading to distinct designs.

For upstream passage, fishways must dissipate the hydraulic head (difference in water level between the headpond above a dam and the tailrace below it). In the absence of roughness elements, this head translates swiftly to velocities that are impassable to any species. Most upstream fishways dissipate this head using either a series of baffles or weirs and pools. As water flows down the fishway, the roughness elements impart friction and turbulence, converting the potential energy of the initial head into heat and noise (Castro-Santos and Haro, 2006; Clay, 1995).

The design of upstream fishways and technical culverts is predicated largely on the anticipated swimming performance of the fish species it is intended to pass. In practice, however, engineers typically use data on swimming ability for these designs. This is because although data on swimming ability are widely available in the literature, data on actual performance are comparatively rare (Castro-Santos and Haro, 2006; Table 1). Additionally, fishways often have areas with velocities that exceed maximum sustained speeds, interspersed with pools where fish can recover between bouts of anaerobic swimming. It is unclear, however, if these design criteria function as intended for most species; this may be one factor that contributes to a widespread failure of upstream fishways to pass fish effectively (Bunt et al., 2012, 2016; Noonan et al., 2012).

Ideally, fishways and culverts are designed using empirical data on endurance and swimming performance of target species, for example, the maximal distance a species can traverse under a range of flow velocities and environmental conditions (Castro-Santos, 2004; Haro et al., 2004; Weaver, 1963). The design of roughness elements in fishways and culverts may also benefit from considering empirical data on fish kinematics, such as lateral body amplitude during movement (Di Santo et al., 2021; Duguay et al., 2018a).

Another factor that likely contributes to passage success being poorer than expected is that most swimming performance studies are conducted in environments where turbulence is deliberately minimized (Brett, 1964), while most upstream fishways and culverts equipped with baffles or corrugations are specifically designed to dissipate energy through the generation of turbulence (Duguay et al., 2018a,b). While we know of no standard guidance for turbulence structure within fishways and culverts, there is broad recognition that turbulence is important, prompting agencies to size pools and structures such that they remain below specific thresholds of energy dissipation (sometimes called the “energy dissipation factor” or *EDF*), which, depending on structures and species typically ranges from 25 to 240 W m⁻³ (Towler et al., 2015).

While *EDF* provides a measure of energy dissipation derived from first principles, it does not provide details on the characteristics of the associated turbulence. Turbulence is a generic term referring to temporal fluctuations in flow velocity and direction. The characteristics of those fluctuations vary widely, however. At its onset, turbulence comprises vortices (eddies) that vary in intensity, periodicity, orientation, and scale (Lacey et al., 2012;

Tritico and Cotel, 2010). In simple cases, these eddies can be highly structured and reduce the energetic costs of fish locomotion (Liao, 2007; Liao et al., 2003a,b). Although this has been demonstrated in laboratory settings, conditions in the field are rarely as simple. Instead, particularly at high flow velocities, eddies interact and create a highly chaotic structure that reduces swimming efficiency and increases energetic costs (Enders et al., 2003, 2005). Complicating matters further, turbulence does not arise spontaneously but instead is associated with structures, typically located on the channel substrate (e.g., boulders, baffles, corrugations). In some cases, fish can shelter behind these, occupying zones of low-velocity and turbulence (Duguay et al., 2018b; Goerig et al., 2017; Wang and Chanson, 2018). This can enable some individuals, particularly those with smaller body sizes, to traverse otherwise impassable barriers (Goerig et al., 2016). This complexity makes the study of turbulence in the context of swimming ability as challenging as it is important (Duguay et al., 2018b; Enders et al., 2017; Hinch and Rand, 2000), and researchers have called for improved standardization of its measurement in association with fish passage (Castro-Santos et al., 2009; Lacey et al., 2012).

One solution to eliminating hydraulic conditions that exceed swimming performance is to use mechanical means to lift the fish past a barrier. This can take the form of a “fish lift,” a sort of elevator that attracts fish into a hopper, then raises them along with a volume of water to the headpond (or sometimes a trucking or similar transport facility), where they are then deposited above the dam (Sprankle, 2005; Travade and Larinier, 2002). Alternatively, navigation locks or specifically-designed fish locks use a similar approach, simply regulating the water level within a chamber to allow passage without requiring fish to ascend a channel volitionally (Júlio Júnior et al., 2009; Travade and Larinier, 2002). While these methods can bypass the limitations of swimming ability, they still require the fish to enter the structures volitionally and remain there while the operation is executed. Although once contained within the structure swimming performance is no longer relevant, conditions below these structures (particularly locks, which must discharge large volumes of water) can be energetically costly. Because of this, passage through locks tends to be poorer than through fishlifts (Finger et al., 2020; Travade and Larinier, 2002). These structures may also create problematic routes of passage for invasive species, as discussed further below.

Downstream fish passage presents engineers with a different suite of challenges. The original work to develop estimates of maximum sustained speeds was intended to determine the maximum flow velocity that downstream migrating salmon smolts could resist at the intakes of hydroelectric dams and other water withdrawals (Brett, 1962, 1964). The thinking was that if velocities could be maintained below U_{ms} salmon would not volitionally pass into the turbine intakes, giving them time to find an alternate and safe route of passage.

Because downstream migrants tend to follow the flow, downstream fishways (often called bypasses) are typically placed close to the turbine intakes. Extensive hydraulic and behavioral studies have shown that flow fields can be manipulated to guide fish to safe passage routes (Bates and Vinsonhaler, 1957; Haefner and Bowen, 2002; Kynard and Horgan, 2001; Shepherd et al., 2007). Then, by regulating the rate of flow acceleration, fish can be enticed to enter these structures. When properly designed, these can entrain fish beyond a point where they are no longer able to sprint out of the structure (Adams et al., 2014; Haro et al., 1998; Kemp et al., 2005) and are conveyed in a jet of water that discharges into a plunge pool of sufficient dimensions to allow for rapid passage without injury (Castro-Santos et al., 2020; USFWS, 2019). Because downstream migrants tend to follow the flow, downstream fishways typically require large discharge. This is inconvenient, because recent work has shown that upstream fishways can be safe conduits for downstream passage, provided that fish can be enticed to enter them (Celestino et al., 2019; Gutfreund et al., 2018), but actual usage is low (Pelicice and Agostinho, 2012).

Despite the extensive efforts and expense applied to the development of fishways and the design of culverts, the performance of these structures is highly variable (Bunt et al., 2012, 2016), and they frequently fail to meet management objectives. While it is common to attribute this to excessive emphasis on a few anadromous species in their initial design, the interplay between fish swimming behavior and ability likewise bears greater scrutiny.

The ability of fish to pass instream barriers in an upstream or downstream direction depends on their locomotor ability, but also on various behavioral aspects such as their motivation to approach, enter and pass a given structure, as well as the strategies employed to navigate challenging hydraulic conditions. The motivation, or willingness to swim (Table 1), can be captured by quantifying the rates at which fish approach and attempt to enter fishways or culverts (Castro-Santos, 2004; Goerig and Castro-Santos, 2017). These rates may depend upon multiple biological (fish species and body size), hydraulic (flow depth and velocity), and environmental factors (temperature, time of day) (Goerig et al., 2020; Goerig and Castro-Santos, 2017; Mensinger et al., 2021). Fish also use behavioral strategies to deal with challenging conditions. They may adopt an exploratory behavior at first then stage repeated attempts to pass a barrier, in which case their probability of success increases with the number of attempts (Castro-Santos, 2004, 2006). They may also optimize their average groundspeed to maximize the distance traversed (Castro-Santos, 2005), or take advantage of turbulence and heterogeneity in hydraulics to select low-velocities areas and move forward without incurring excessive energy costs (Goerig et al., 2017; Wang and Chanson, 2018). It is therefore important to also consider locomotor behavior in fishway and culvert design, and how behavior and ability are related to actual hydrodynamics near and within fish passage structures.

3 Invasive species in river systems

Industrialization, commerce, and transportation systems have provided numerous and novel vectors for conveying species across what were once impermeable barriers of elevation, distance, salinity, temperature, etc. While some of these invasions are the consequence of deliberate introductions gone astray (such as the introduction of Brown Trout (*Salmo trutta*) to North America, and Brook Trout (*Salvelinus fontinalis*) to Europe and western North America (Rahel et al., 2008)), others were purely accidental, either via escapement from aquaculture facilities (e.g., Bighead (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*) in the Mississippi drainage (Stokstad, 2003)), and in ballast water (Elskus et al., 2017; Treanor et al., 2017), etc.). In some cases, multiple pathways interact, and the success of invasions is mediated both by the vector of transmission and by habitat type and quantity (freshwater habitats are much more vulnerable to invasion (Alcaraz et al., 2005; Beletsky et al., 2017; García-Berthou et al., 2005)).

Navigation has been a major catalyst for these invasions, both in the form of ballast water, and via navigation locks. While ballast water vectors can be mitigated by purging and replacing ballast tanks during transit and chemical treatments (Elskus et al., 2017), this is not true of navigation locks. Locks are pervasive throughout the rivers of the developed world, and have promoted the invasions of Round Goby (*Neogobius melanostomus*) in the Rhine (Roche et al., 2013), invasive carps in the Mississippi and bordering drainages (Stokstad, 2010), and Sea Lamprey (*Petromyzon marinus*) into the Laurentian Great Lakes (Zielinski et al., 2019), to name but a few examples. Novel technologies are in development to limit movements through these pathways, although to date no measure has proven to be effective (Stokstad, 2003, 2010; Zielinski et al., 2019).

Once established, invasive species are exceedingly difficult to control, let alone eradicate. One case in which control can be possible is when invasive species are migratory, using discrete habitats for spawning and growth (Behrens et al., 2017). In this situation, barriers that inhibit movement can be constructed to prevent passage, interrupting key life history stages. In lotic habitats, such efforts sometimes focus on swimming ability and behavior, although these efforts are not always successful: interest in separating Brown Trout and Brook Trout were frustrated by the striking similarity in swimming ability between these two species (Castro-Santos et al., 2013). In the case of Sea Lamprey in the Great Lakes, however, considerable success was achieved by constructing hundreds of barriers on surrounding tributaries.

These barriers were designed to prevent invasive Sea Lamprey from passing, but at sufficiently low heights that highly-valued salmonids were able to pass (Zielinski et al., 2019). This was facilitated by both the ability and propensity of salmonids to leap over obstacles. There was an unintended consequence, however: many non-leaping native species also migrate between the

lakes and rivers to spawn and for other activities important to their life history, and these barriers have obstructed these movements (McLaughlin et al., 2013). Current solutions to this dilemma include trap-and-sort facilities, where lamprey are culled from fishways and native species are allowed to proceed upstream (Pratt et al., 2009).

Owing to the overall poor performance of fishways at passing native species, this solution has been deemed inadequate, and significant efforts are underway to develop fishways that selectively block Sea Lamprey while allowing native species to pass (Fig. 3; Zielinski et al., 2019; <http://www.glf.org/fishpass.php>).

Owing to their unique morphology, Sea Lamprey are thought to have reduced swimming ability compared with native species. This suggests that a simple velocity barrier might be a successful approach to selective passage, at least for some strong swimming species (Fig. 4).

However, lamprey have a secret weapon: their sucking disc, used to attach to their prey and for constructing spawning redds, is also an efficient tool for ascending zones of high-velocity flow (Fig. 3). During attachment, the only actual work being performed is the maintenance of sufficient suction to prevent the fish from being dislodged. In this way, they are able to recover from bouts of sprinting and, when ready, to execute another burst of swimming (Castro-Santos et al., 2019). By incrementally sprinting and attaching to a range of substrates they are able to ascend challenges that are impassable by almost any other species (Moser et al., 2011).

This unique ability can be countered by lining channels with a substrate that inhibits attachment. Some studies have shown that this is a promising line of research, although definitive solutions remain elusive (Castro-Santos et al., 2019; McCauley, 1996; Zielinski et al., 2019), and other approaches will be needed for smaller-bodied and weaker-swimming species. Nevertheless, these and similar efforts hold promise for helping to limit access to key habitats and facilitating control. Lessons learned from lamprey may hold clues for the control of other species with related abilities, such as Round Goby (Voegtle et al., 2002; Webb, 1989).

4 Capture fisheries

4.1 The biomechanical foundation of fish capture

Global fisheries production was 178.5 million tons in 2018, with 96.4 million tons from capture fisheries (FAO, 2020). Fish are an important source of nutrition for many countries, providing 3.3 billion people globally with 20% of their animal protein intake in 2018 (FAO, 2020). Fish capture is an essential activity in many nations, especially in coastal and island nations, with a large variety of fishing gears and operational methods, and these uses are likely to continue (He et al., 2021a).

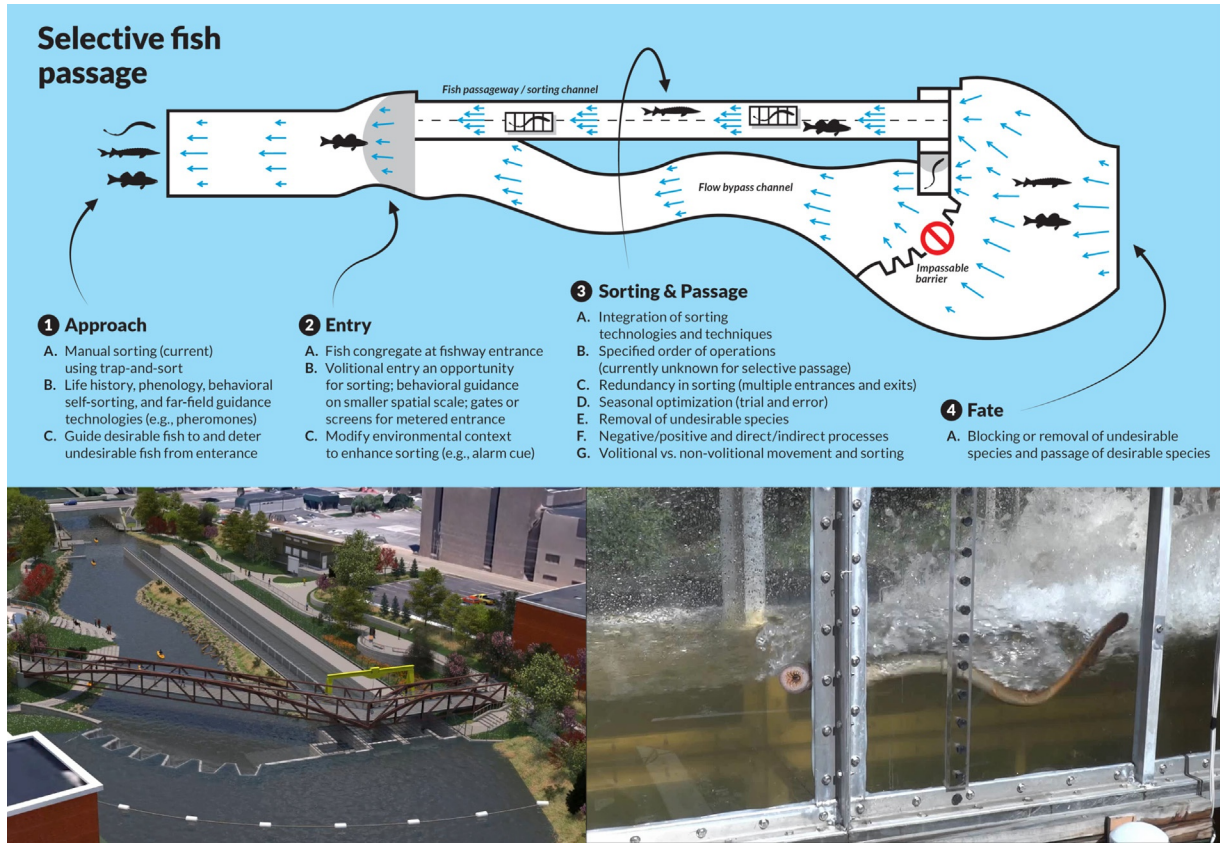


FIG. 3 FishPass design drawing and lamprey attached to the wall of an experimental flume. Upper and lower-left panels: the FishPass is a multinational collaboration to develop structures that will selectively pass a range of native fish while obstructing Sea Lamprey. The ultimate intent is to use intrinsic differences in morphology, capacity, and behavior to separate and remove invasive Sea Lamprey while permitting free passage to native species. The design will allow use of free-swimming fish in a field-like setting, while allowing sufficient control to conduct experiments as they pass through the three phases of fish passage: (a) discovery of (or approach to) a potential passage route; (b) entry into the passage structure; and (c) passage through the structure itself. Each of these steps offers an opportunity for failure: passage is only possible by sequentially completing all three phases (Castro-Santos and Haro, 2010; Silva et al., 2018). Lower-right panel: a Sea Lamprey attached to a plexiglass wall in a flume in high-velocity flow (photo by E. Goerig, USGS).

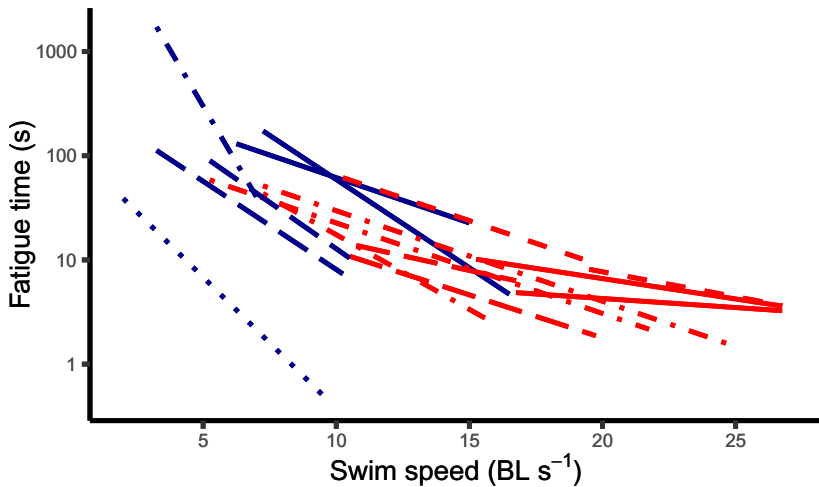


FIG. 4 Comparative sprinting (red) and prolonged (dark blue) endurance curves for a range of species from five orders: Cypriniformes (Iberian barbel (*Luciobarbus bocagei*), straight-mouthed nase (*Pseudochondrostoma duriense*), and white sucker (*Catostomus commersoni*), solid lines); Clupeiformes (American shad (*Alosa sapidissima*), Alewife (*A. pseudoharengus*), and Blueback Herring (*A. aestivalis*), dash-dot lines); Perciformes (Walleye (*Sander vitreum*) and Striped Bass (*Morone saxatilis*), long-dashed lines); Salmoniformes (Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*), short-dashed lines); and Petromyzontiformes (Sea Lamprey (*Petromyzon marinus*), dotted line) (Castro-Santos, 2005; Castro-Santos et al., 2013; Sanz-Ronda et al., 2015; Zielinski et al., 2019). Sea Lamprey have comparatively poor endurance, but their ability to attach to surfaces (Fig. 3) enables them to recover from fatigue without being swept downstream in strong currents.

Given the importance of both commercial and subsistence fishing, it is becoming increasingly important for managers to regulate both the species and sizes captured by fishing gears. In many cases, it is important to selectively target a given size and species in order to optimize future recruitment (Beverton and Holt, 1957). The required selectivity is often not matched by gear performance, however, and vast quantities of fishes and other organisms are unintentionally captured as bycatch and then discarded at sea, often with serious ecological and social consequences (Harrington et al., 2005). Because of this, as well as owing to the associated benefits to the fishers themselves, extensive efforts are underway to improve efficiency and selectivity of fishing gears (Hasselman et al., 2016; He et al., 2021b; Valdemarsen, 2001).

Fishing gears are designed based on the behavior and locomotion ability of target species, and more recently, that of unwanted bycatch species and protected species. Fish locomotion is an important factor in the design and operation of the active gear to catch or release fish, such as trawls, purse seines, and dredges (He, 1993; Wardle, 1986). For passive gears such as gillnets and longlines, swimming activity determines the range of their fishing area, which also directly impacts capture efficiency (He, 2003).

Fishing is the interaction of fish and fishing gear in a physical environment. Environmental conditions affect biology, ecology, and physiology of fish, which governs fish reaction to fishing gears, as well as their ability to escape from them. Environmental conditions also directly impact the type of fishing gear that can be operated. Successful fish capture is managed by using the appropriate fishing gear to catch the intended fish (species and size) at the appropriate time and place (Fig. 5).

4.1.1 Fish capture by trawls: The role of fish locomotion

Understanding fish biomechanics, especially swimming ability and behavior, is crucial in active fishing gears that chase or surround fish for capture, but it is also important for passive fishing gears that rely on fishes' movement into the gear. Here, we take the single boat bottom otter trawl (He et al., 2021a,b; called "otter trawl" or simply "trawl" hereafter), one of the most common active gear types, as an example on how swimming behavior and ability thread the entire capture process from the time the fish is aware of the approaching trawl to the time it is either retained in the codend or has escaped from the trawl. Fig. 6 illustrates the capture process of fish by a trawl. The trawl as well as its influenced area is divided into five zones where fish may behave differently during the capture process.

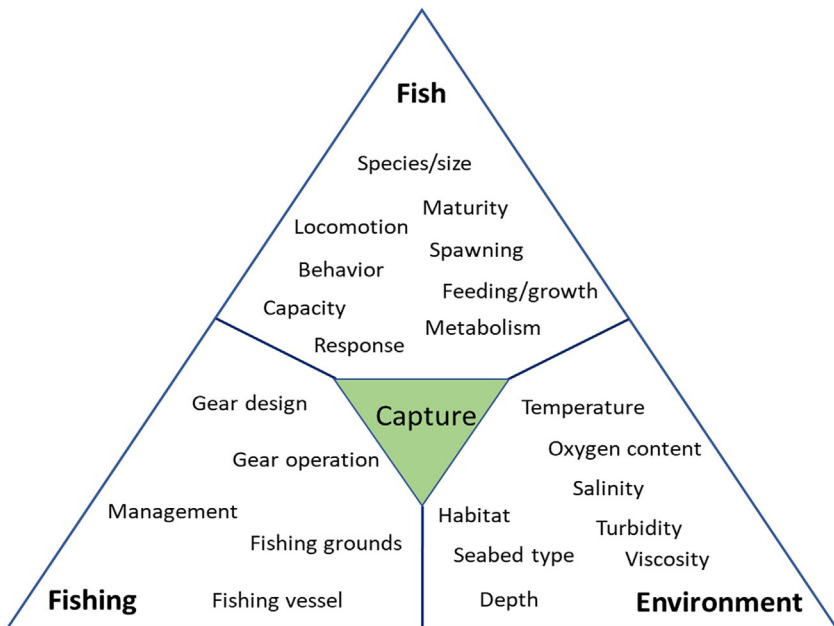


FIG. 5 Three pillars for fish capture. Successful fish capture is about using the right fishing gear to catch the right fish (species and size) at the right time and place.

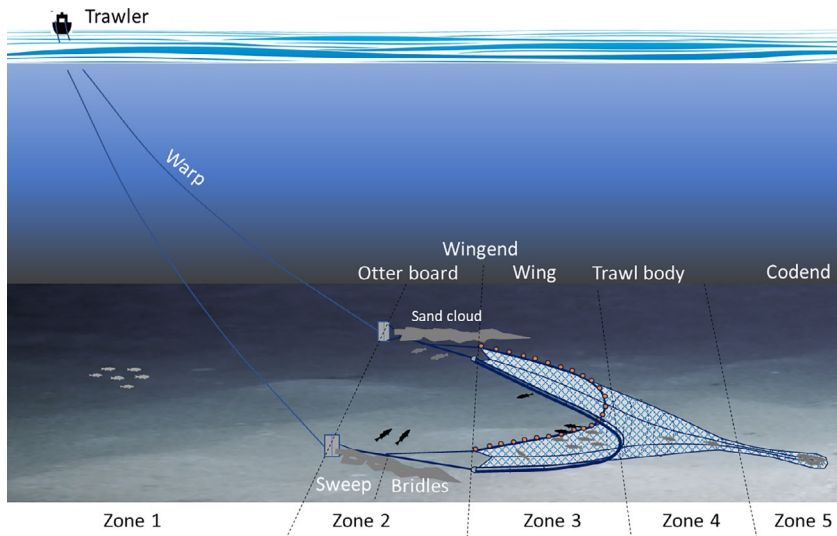


FIG. 6 Typical swimming behavior of fish when approaching and being herded inside an otter trawl. Zone 1 is the pre-trawl zone where fish are alerted of an approaching otter trawl through acoustic and visual stimuli from the trawl. Zone 2 is the herding zone where fish are herded by sweeps and bridles toward the mouth of trawl between the wings. Fish are typically moving away from the towed oblique rope toward the center of the trawl path. The shaded area trailing the otter board are sand clouds. Zone 3 is the concentration zone where fish are concentrated toward the center of the trawl, and turn and swim with the trawl. Zone 4 is the trawl body that gradually narrows and guides fish toward the codend. Zone 5 is the codend, which is often preceded with an “extension piece.” Fish are accumulated in the codend where turbulence and motion of the codend stimulate fish to attempt to escape through the meshes.

Zone 1 is the pre-trawl zone, which could extend forward for more than a kilometer from the otter boards. Depending on the type of seabed and the design of the trawl, noises generated by the otter board hitting rocks on the seabed and from the propellor of the trawler can be heard by fish far earlier than the fish can see the trawl. Using stationary hydrophones, Winger (2004) demonstrated that Atlantic Cod (*Gadus morhua*) responded to a survey trawl vessel at 1500m by slowing their swimming speed to near zero. Acoustic stimuli from the trawler and its trawl may thus raise awareness in the fish, which may look for possible dangers well before the trawl becomes visible (Wardle, 1986).

Zone 2 includes the area from the otter boards to the wingends. For many fish trawls, especially trawls for flatfish, long cables (sweeps and bridles) connect the boards and the wingends to increase the horizontal distance between boards (called door spread). Bridles usually refer to two or more cables that extend from top and lower wingends. They are joined together and connect to the sweep.

Fish often react to moving oblique cables by swimming away from them and are herded toward the path of the trawl. The angle between the cable and the towing direction is called the sweep angle (α in Fig. 7), while the

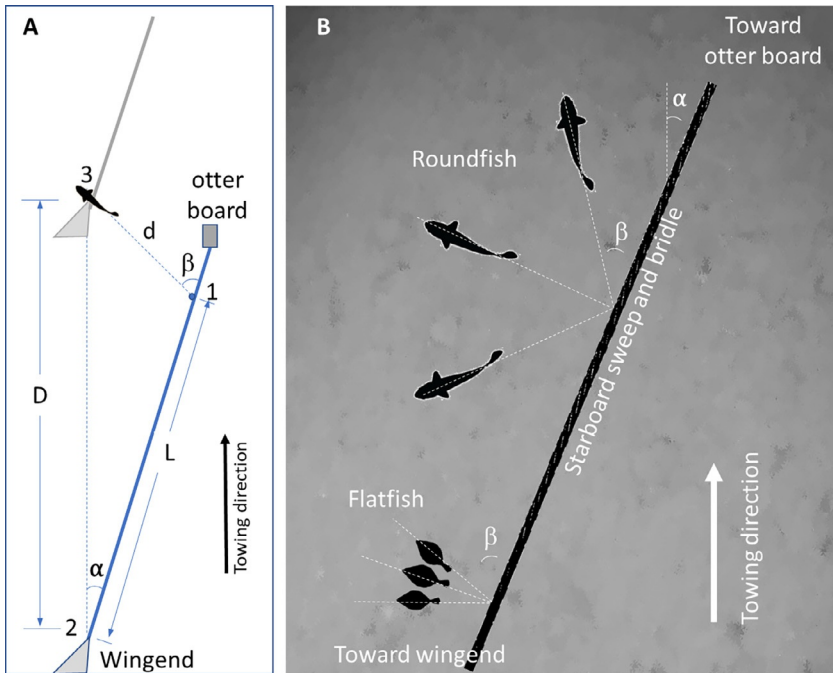


FIG. 7 Fish reaction to sweeps and bridles of a bottom otter trawl. (A) A fish at Position 1 has to be capable of swimming to Position 3 before the wingend moves from Position 2 to 3 for it to be herded into the path of the trawl between the wings. (B) Avoidance angle of fish. Typically, roundfish have a larger range of avoidance angles (β) than flatfish which are usually at around 90 degrees.

angle between the direction of fish avoidance behavior and the cable is the avoidance angle (β in Fig. 7). For fish at Position 1 (ahead of the path of the bridles, but outside of the capture zone defined by the wings, Fig. 7) to be herded into the capture zone, they have to swim the distance (d in Fig. 7) from Position 1 to Position 3 within the time period when the wingend moves forward the distance (D) from Position 2 to Position 3. Swimming speed required (U_s) is related to angles α and β , and to the towing speed of the trawl (U_{Tr}). The endurance time (Table 1) required for a fish to be herded into the trawl path (T_{esc}) is related to α , β , U_{Tr} , as well as to the position of the fish along the length of the cable when fish starts to react (L).

$$U_s = U_{Tr} \frac{\sin(\alpha)}{\sin(\beta)} \quad (1)$$

$$T_{esc} = \frac{L}{U_{Tr}} \frac{\sin(\beta)}{\sin(\beta - \alpha)} \quad (2)$$

Towing speed of the trawl and sweep angle directly affect the swimming speed required for herding. Simulations from Eqs. 1 and 2 with a trawl towing speed of 1.5 m/s and reaction distance of 100 m from the wingend are plotted

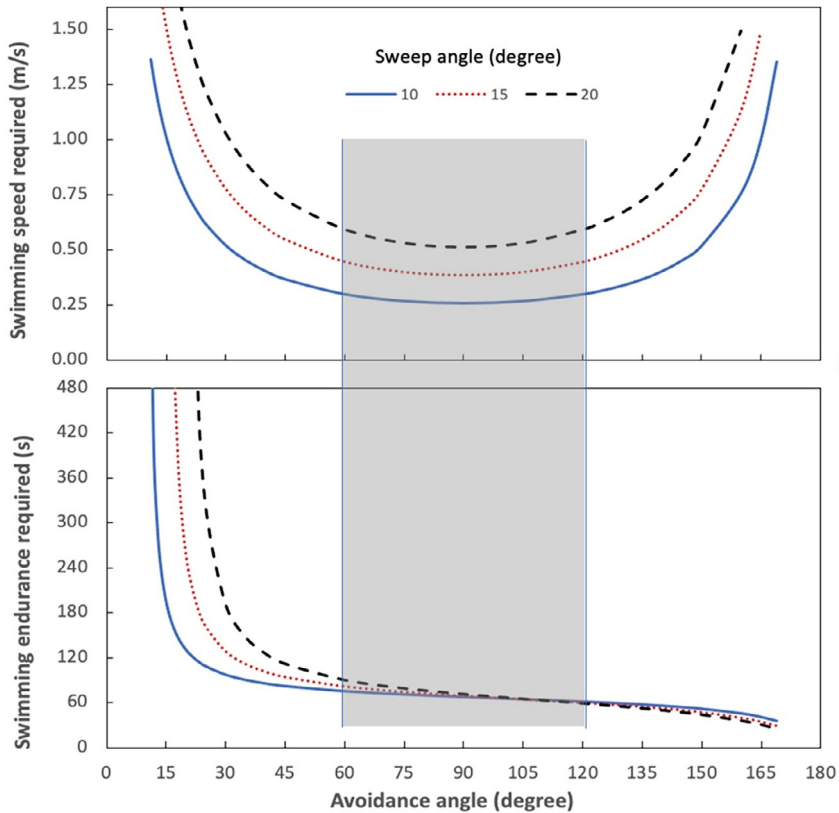


FIG. 8 Swimming speed and endurance required for fish to be herded into the path of trawl as related to sweep angle and avoidance angle for fish that react to a cable towed at 1.5 m/s at 100 m from the wingend.

in Fig. 8. Typically, the lowest swimming speed required is when the fish avoids the trawl by swimming directly away from the cable ($\beta=90^\circ$), but the changes in the required swimming speed are minimal from 60° to 120° (shaded zone, Fig. 8). Larger and smaller avoidance angles require higher swimming speeds for fish to be herded into the trawl path; if a fish is not capable of doing so, it will be overtaken by the sweep and not herded.

Sweep angles (α) of otter trawls are typically between 10° and 20° . Large sweep angles require fish to swim faster to be herded into the trawl path, which may prove inefficient for catching some fish. Sweep angle $>20^\circ$ was found to reduce catch of Cod and Haddock (Strange, 1984), indicating the importance of matching design and mechanics of the fishing gear with biomechanics of the target fish species.

Fish reacting to longer sweeps are required to swim longer to get away from the cable and into the path of the trawl, which may be challenging for

species with lower swimming endurance. As swimming endurance is related to the length of fish (He and Wardle, 1988), among other factors, longer sweeps may result in the catch of more large fish and fewer small fish. Indeed, Engås and Godø (1989) found that longer sweeps resulted in a higher proportion of large Atlantic Cod and Haddock in survey trawls.

Avoidance angles of roundfish (with fusiform or laterally compressed shape) such as Atlantic Cod, Haddock (*Melanogrammus aeglefinus*) and Pollock (*Pollachius virens*) are more variable than those of flatfish, which are more consistent and closer to 90° (Fig. 7). Through underwater telemetry, researchers in Scotland found that Haddock approached and avoided the sweep at larger and more varied angles and at greater distance from the cable (SOAFD, 1998). Flatfish often react at a very short distance from the cable, exhibiting a swim-and-rest behavior, as being periodically “chased” by the approaching cable (Wardle, 1986; Winger et al., 2010).

Zone 3 (Fig. 6) includes the area between the wings and under the square (overhang) of the trawl, just ahead of the groundgear, which contacts the seabed. Fish arriving at Zone 3 typically start to turn and swim with the trawl, with flatfish swimming much closer to the groundgear. The swimming ability of the fish and the towing speed of the trawl strongly influence the duration that fish swim with the trawl in that area.

The variation in swimming ability with body size and species has important implications for selective fishing (He and Wardle, 1988; Wardle, 1977; Wardle and He, 1988). For example, 40 cm-long Saithe (also called Pollock, *Pollachius virens*) can swim for 6 min at 1.5 m/s before being captured by a trawl, while Haddock, Whiting (*Merlangius merlangus*), and Atlantic Cod of similar sizes could only maintain that speed for 2.5, 1 and 0.5 min, respectively. By comparison, endurance of smaller individuals of these species was <1 min at the same towing speed of 1.5 m/s (Main and Sangster, 1981).

Atlantic Mackerel (*Scomber scombrus*, 35–45 cm in length), being a fast swimmer, was observed swimming forward and escaping from the groundfish trawl towed at 1.5 m/s (Main and Sangster, 1981). Midwater trawls targeting Atlantic Mackerel are typically towed much faster, ranging from 1.9 to 2.3 m/s. Even at these high speeds, Mackerel (34 cm) were swimming for 30 to 58 min with a midwater trawl as observed by an underwater camera system (Rosen and Holst, 2013). By comparison, in the laboratory, Atlantic Mackerel of similar size were able to swim at 1.5 m/s for 60 min and at 1.8 m/s for 10 min (He and Wardle, 1988). It must be pointed out that observations at sea of fish swimming speed and duration are opportunistic and often lack precise details of fish size and physiological status (e.g., the level of exhaustion).

Subtle changes in towing speed can make important differences in capture efficiency. Some species will maintain a position just ahead of a trawl and evade capture. To respond to this behavior, a fishing strategy called “power take-off” is sometimes practiced to catch the unexhausted fish by increasing

the towing speed at the end of the tow. Conversely, towing speed may be reduced before hauling to avoid catching stronger-swimming fish.

Zone 4 includes the body of the trawl net (Fig. 6), where fish are gradually funneled within the reduced diameter of the net. Fish that have given up swimming in front of groundgear may swim toward the codend, but they may also orient forward again as space becomes narrower. Longer nets can better guide fish toward the codend with less meshing of fish in the net.

Zone 5 is the codend of the trawl where fish are accumulated (Fig. 6). A codend with accumulated catch can block the water flow and create turbulence within the codend. Fish arriving in the codend may start to swim again, at slower swimming speed due to the bucket effect created by the codend with fish. Fish may also attempt to swim out through the open meshes, which may cause scale loss or injuries due to contact with the mesh. He (1993) modeled escape probability of fish through a codend mesh under different towing speeds, mesh sizes, and water temperatures, revealing a higher probability for fish to escape without contacting the netting when the codend has a large mesh size, the towing speed is low, and in areas with warmer waters.

4.2 The role of fish biomechanics in reducing bycatch and discards: A case study

While the definition of bycatch varies among jurisdictions, it generally refers to “the catch of organisms that are not targeted” (Perez Roda et al., 2019). Tropical shrimp trawls in the Gulf of Mexico faced bycatch of sea turtles and juveniles of important commercial fish species such as Red Snapper (*Lutjanus campechanus*). While sea turtle bycatch was significantly reduced through the testing and introduction of various turtle excluder devices (TEDs, also called trawl efficiency devices) in the 1980s and 90s (Jenkins, 2012; Watson et al., 1999), fish bycatch persisted. Researchers in the Gulf of Mexico have conducted a series of studies on topics ranging from behavior of relevant species to gear designs to reduce fish bycatch in shrimp trawls in the last 30 years. The effort led to the development of several types of bycatch reduction devices (BRDs), such as the fisheye, the extended funnel, and the Jones/Davis device (Watson et al., 1999). This case study describes the process and results of the development of the nested cylinder bycatch reduction device (NCBRD), designed to reduce red snapper bycatch through understanding of its biomechanics, especially swimming behavior and ability.

Underwater observations of red snapper found that fish would seek areas of low flow near the bycatch reduction device (BRD), which may provide opportunity for fish to escape from the opening of the device, but very few fish escaped during steady towing of the trawl (Engås et al., 1999). However, as the trawl was slowed during hauling, significant active escape occurred. Due to variabilities in haulback procedures, the rate of bycatch reduction varied among vessels. Understanding the mechanism of fish escape and means to induce fish to escape was thus proposed (Engås et al., 1999).

To further understand swimming behavior of red snapper, Engås and Foster (2002) conducted a laboratory study to examine the effect of “inclined” water flow. When the recirculating swimming tunnel was horizontal, red snapper 9.7–14.4 cm in length maintained a specific position (called bull’s eye) while swimming steadily against a flow velocity of 3 body lengths per second (BLs^{-1}) for 10 min. When the swimming tunnel was tilted (as much as 45°), many fish were not able to maintain the same position and instead showed erratic swimming behavior such as moving up, down and sideways, demonstrating the potential of utilizing inclined water flows to develop more selective devices (Engås and Foster, 2002).

Critical swimming speed (U_{crit}) of red snapper was measured in laboratory at various times of the year, showing a peak in October; importantly, diel period (day and night) did not affect swimming performance (Parsons and Foster, 2007). However, when exposed to a vortex generating bycatch reduction device, significantly larger percentage of fish escaped during the day (higher luminosity) than during the night. Moreover, when light was provided in the test tank (e.g., using a green Cyalume light stick or blue-green LED light), all fish escaped within a short period of time, with the intensity of light negatively correlated to the time they took to escape (Parsons et al., 2012). This indicates that illumination during nighttime trawling can be an effective way to stimulate escape behavior of bycatch species (Parsons and Foster, 2007).

Parsons and Foster (2007) also tested the preference of illuminated and unilluminated area in a water tunnel. They found that all fish chose the darker side of the swimming tunnel, indicating negative phototactic response. This provides additional evidence that fish behavior could be partly controlled by manipulating illumination, especially for shrimp trawls in the Gulf of Mexico, where most fishing operations are conducted at night (Parsons and Foster, 2007).

Based on the above and other research, Parsons and his colleagues designed a BRD called nested cylinder bycatch reduction device (NCBRD), as illustrated in Fig. 9 (Parsons and Foster, 2015; Parsons et al., 2012). The NCBRD modifies the flow in the area outside of the inner section and provides illumination at the exit from the mesh sock, allowing Red Snappers to turn and escape. The targeted shrimp species, which have inferior swimming ability than Red Snapper, are pushed to the codend. This design reduced red snapper bycatch by as much as 50% (Parsons and Foster, 2015).

5 Fisheries management and enhancement

5.1 Fisheries surveys

Bottom trawls are the most common fishing gear for fisheries surveys, but pelagic trawls, gillnets, longlines, and pots are also used. Acoustic devices such as echo sounders are used for surveying schooling fish in pelagic environment. In rivers and streams, electrofishing is also used for surveys. More recently, stationary underwater cameras are used to survey coastal and reef fish. While most of these survey methods may be affected by fish behavior,

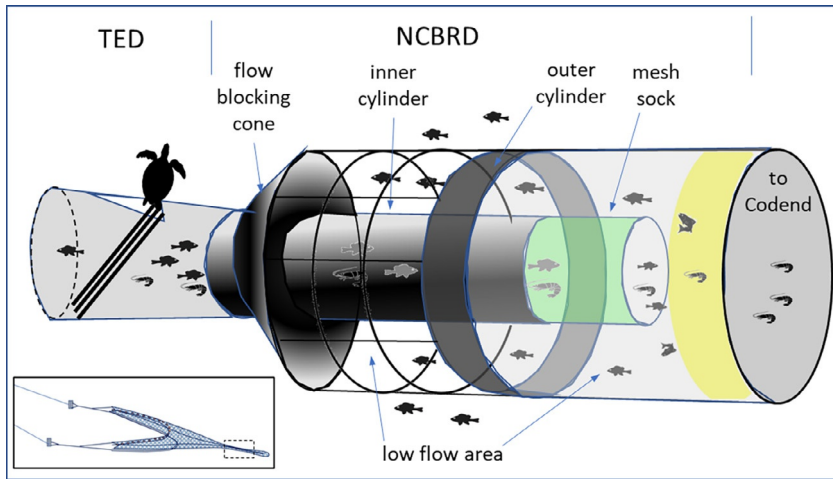


FIG. 9 Schematic drawing of the nested cylinder bycatch reduction device (NCBRD) designed for the Gulf of Mexico and Southeast US shrimp trawl fisheries. The flow-blocking cone reduces flow in the area outside of the inner cylinder. The rear of the exit area is illuminated (yellow). Red snappers turn at the exit area of the mesh sock and seek the low-flow and darkened area, leading to escape in the area between the cone and the out cylinder where there is no netting. Shrimps with poor swimming ability are pushed to the codend. Redrawn based on [Parsons et al. \(2012\)](#) and [Parsons and Foster \(2015\)](#).

especially locomotory habits, we offer the following examples to illustrate how fish biomechanics, especially swimming behavior can affect outcome of fisheries surveys.

5.1.1 Tow duration of bottom trawl surveys

Tow duration of bottom trawl surveys is usually between 15 and 60 min. Evidence had previously been interpreted as indicating there was no effect of tow duration on catch per unit effort (CPUE: [Godø et al., 1990](#); [Walsh, 1991](#); [Wieland and Storr-Paulsen, 2006](#)). More recent data challenge this view: [Sala \(2018\)](#) found an effect of tow duration on CPUE as well as the size of fish, comparing 30 and 60 min tows. This likely occurs because of the relation between swimming performance and body size: larger fish may not become exhausted when swimming at the mouth of trawl if their endurance exceeds tow duration. It is thus possible that large fish may be underrepresented when the tow duration of a survey trawl is short. Effect of tow duration on CPUE and size distribution of the catch may be species specific, and more information may help to better-inform design of bottom trawl surveys.

5.1.2 Encountering probability of fish with passive survey gears

Catch by passive gears (also called stationary gear, or fixed gear) such as gill-nets, longlines, and pots rely on the movement of fish which accidentally

swim into gillnets, or are attracted to bait in longlines and pots. For gillnets, the faster a fish moves, the more likely the fish will encounter the net, both because of the volume of water encountered (Løkkeborg et al., 2010, 2014; Rudstam et al., 1984), and because of the associated reduction in response time (Engas and Lokkeborg, 1994). Therefore, incorporating probability and speed of fish encountering fixed gear will improve understanding of gear efficiency and hence more accurate stock assessment (Lennox et al., 2017).

5.1.3 Active space in passive survey gears

“Active space” of a passive fishing gear is the potential area within which the fish may be captured by the gear (McQuinn et al., 1988). It is related to the swimming speed of fish and soak time of the gear (the duration the gear is deployed). The effectiveness of these gears varies with season, and it is likely to change as habitats change in response to a warming climate. For example, He (2003) modeled the active space of a gillnet for catching Winter Flounder (*Pseudopleuronectes americanus*) and found that active space would be more than 7 times greater at 4.4 °C than that at -1.2 °C for a gillnet set for 12h, owing to increased activity of winter flounder at the higher water temperature. Similarly, active gears may become less effective in historically colder regions if the species there become more active and swim with greater endurance at higher temperatures, although such changes may be offset by changes in habitat use. Regardless, temperature-related changes in fish activity and swimming ability are likely to result in changes in vulnerability to both active and passive fishing gears, with associated implications for fish capture, stock assessment surveys and management.

5.2 Stock enhancement

Above we describe various approaches to restoring populations impacted by human activities, whether through fragmentation, habitat alteration, fishing, etc. Often, though, it is necessary to supplement populations in the field and/or to maintain broodstock to safeguard existing genetic diversity. To this end, fish hatcheries have served a vital role for more than a century (Anonymous, 1872, 1877; Clift, 1872). The development of dams and targeted harvest of migratory species, particularly in North America during the 18th and 19th centuries were recognized as important causes of declines in many species. This context, combined with the opening of vast territories of what became public lands and waters prompted significant public investment in the artificial propagation and stocking of both native and non-native species into freshwater lakes and streams (Anonymous, 1877).

The captive rearing of fish has a much deeper history; however, aquaculture has been an important food source for humans for millenia. The earliest records of aquaculture for food production come from China in 3500 BCE; where by the 1980s 2.7 million hectares of freshwater surface area were

dedicated to aquaculture for food production (FAO, 1983). The importance of aquaculture continues to grow and will likely remain one of the most important sources of human dietary protein (Teletchea and Fontaine, 2014).

As with many species raised in captivity, freedom of movement and exercise has benefits, both for the health of individual fish and for the quality of the final product, whether it be destined for restoration of wild populations or for food markets. When compared with fish raised under lentic conditions, a range of species subjected to flows on the order of 1 BL s^{-1} show increased feed conversion rate, improved growth rates, better fin condition, added mass and changed composition of both red and white muscle, increases in number of dermal layers, and improved shelf life. Not surprisingly, some species show improved survival and fitness, as well as more natural movement patterns when subsequently released to the wild following exercise regimes (Davison, 1997; Jobling et al., 1993; Jørgensen and Jobling, 1993).

6 Biomimetic engineering for fish conservation in the anthropocene

One pervasive problem that has impeded development of effective conservation strategies is the difficulty of observing live fish in their native (or invasive) habitat. Physiology is often studied using *in vitro* methods, or as mentioned above, on whole animals constrained in artificial environments that prevent them from performing behaviors and tasks most relevant to their lived reality.

Advances in telemetry, particularly over the past four decades, have dramatically improved our ability to monitor both large- and small-scale movements of free-ranging animals (Monan, 1985; Monan et al., 1975). Development of large, fixed receiver arrays have promoted an increasing number of studies, offering insights into habitat use, effects of human activities, etc. (Krueger et al., 2018).

Characteristics of local environments, and the sheer vastness of aquatic ecosystems can make such methods impractical, however, and technologies are rapidly evolving that will expand the scope of monitoring. One class of devices that is yielding insights is automated drones. Aerial drones, for example, have allowed surveys of land animals and their movements in locations and over distances that are difficult if not impossible to achieve for human observers (Inman et al., 2019; Schlossberg et al., 2016). Drones are also used in studies of bird migration and behavior (Canal and Negro, 2018; Marinov et al., 2016), and are indispensable for habitat surveys, especially in inaccessible areas. These concepts have recently been expanded to the marine environment. Restrictions on survey crews owing to the Covid-19 pandemic created an opportunity to deploy unmanned drones to survey large tracts of ocean for fisheries surveys that had previously only been performed by human-crewed vessels, and similar efforts are ongoing around the world

(De Robertis et al., 2021). In addition to performing autonomous surveys, such devices also offer opportunities to observe fish in their environment and their response to things like fishing gears, promising to greatly improve our understanding of the mechanical underpinnings of gear efficiency, bycatch, and other challenges.

Nevertheless, technological progress in fish conservation biology is lacking for reasons that must include the many challenges involved in operating mechanical systems underwater, difficulty with vision and acoustic communication in aquatic environments, and the inability of most current robotic systems to function with the speed, independence, and maneuverability needed to operate in often challenging high-velocity or turbulent waters.

These challenges, as well as the general benefits that come from physical and quantitative modeling have prompted many researchers to turn to fish biomechanics and functional morphology for inspiration, with some of the more remarkable devices currently being deployed incorporating design concepts inspired by biological systems (Whitt et al., 2020). The development of fish-inspired robotic systems coupled with currently available technologies such as electronic tags and drones promises to greatly improve our ability to both understand and conserve fish populations in the near future. In addition, unexpected benefits can arise for the analysis of fish biology from mechanical and robotic perspectives. Advances such as the use of fish-skin-like skin coverings to enhance propulsion through the water by both human swimmers and ships, and new vehicles that can navigate complex hydraulic and structural environments at depth are examples of benefits that can result from the study of fish locomotion. In this section, we first summarize the current state of fish-inspired robotic platforms that could be further developed to contribute to fish conservation physiology, and then we describe several specific areas where technological approaches are beginning to make particularly valuable contributions.

6.1 Fish robotics: Current state of the art

Many, if not most, fish-inspired robotic systems are small, low speed platforms that are designed as laboratory-based “scientific demonstrators” constructed to better understand the basic physics of aquatic propulsion (Lauder et al., 2012; Moored et al., 2011). Some of these laboratory systems use simple actuation to drive a flexible surface that has been used to understand the effect of body flexibility, tail shape, and stiffness on swimming speed and efficiency (Fig. 10; Lauder and Tangorra, 2015; Van Buren et al., 2017, 2019). One advantage of such experimental platforms, in addition to their relative simplicity, is their utility for exploring a large parameter space of movement and quantifying the effect of swimming objects to uncover how undulatory wave-like swimming motions affect speed and efficiency (Hertel, 1966; Lauder and Tangorra, 2015; Smits, 2019).

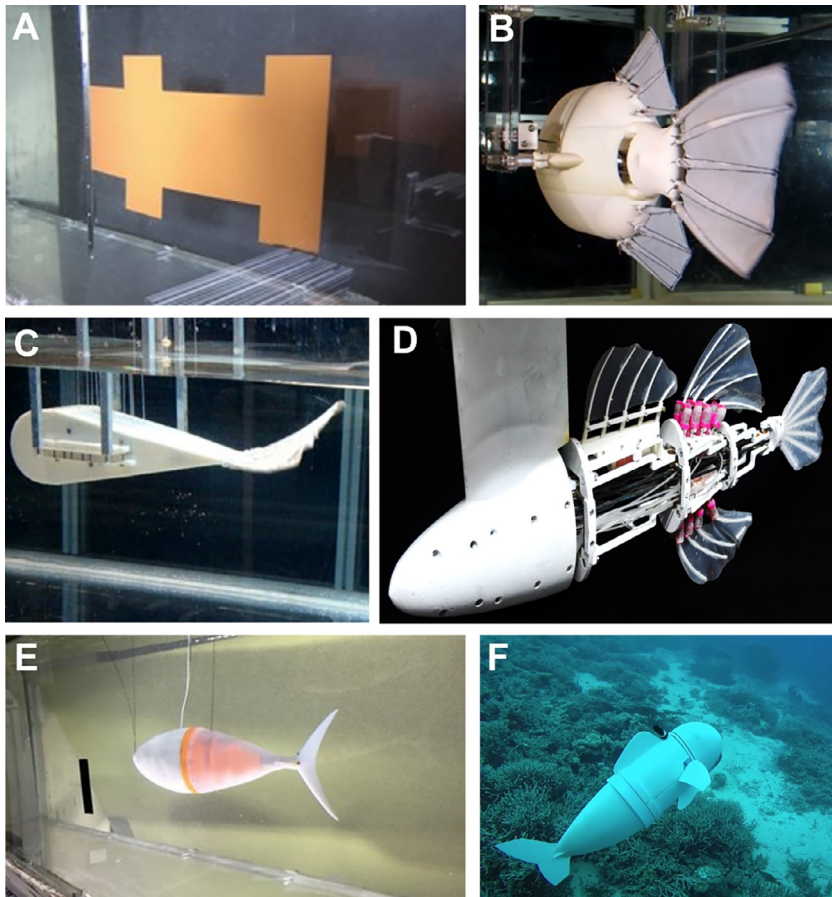


FIG. 10 Current fish robotic systems range from simple flexible plastic models of fish bodies and fins actuated at the leading edge (A) (Matthews and Lauder, 2021) to platforms designed to investigate the function of dorsal, anal, and caudal fins with individually controllable fin rays (B and C: Esposito et al., 2012; Mignano et al., 2019). Whole fish laboratory robotic platforms (D and E) (Wen et al., 2018; Zhu et al., 2019) allow study of the body bending and thrust production during both steady swimming and acceleration behaviors. Katschmann et al. (2018) designed a free-swimming fish robot (F) for marine reef environments that is controllable remotely by a diver.

Another class of laboratory fish-like robotic systems uses mechanical prototypes of fish fins, modeled explicitly on fish anatomy, to explore how fins generate propulsive forces (Fig. 10). Such studies have included the design and analysis of both pectoral fin and caudal fin robots for propulsion and maneuvering (Esposito et al., 2012; Gottlieb et al., 2010; Tangorra et al., 2011). While progress has been made incorporating these fish fin-like actuators into a whole fish robot, such systems have so far been confined to the laboratory. Using highly simplified fin models based on airfoil shapes attached to

a rigid “body” has allowed free-swimming robotic systems to perform well in a swimming pool (Long et al., 2006), but to date such platforms have not been deployed in the field under their own power.

One fish-like robotic system that has been deployed in the field is the SoFi system described by (Katzschmann et al., 2018) who developed a robotic fish using flexible (soft) actuators powered by a hydraulic mechanism. Their explicit goal was to design a robot that could function in marine environments for coral reef exploration (Fig. 10F), and they used acoustic communication from a hand-held controller operated by a nearby diver to control robot trajectory. The SoFi robot is capable of generating tail beat frequencies of up to 1.4Hz and average swimming speeds of 23.5cm/s or 0.5 body lengths/s, and the SoFi robot of Katzschmann et al. (2018) represents the most fish-like, controllable, and field-deployable robotic platform developed so far.

One final area of research interest in the design of biomimetic fish-like swimming systems focuses on the skin and specialized surface structures that could enhance swimming performance. Fish exhibit a remarkable diversity of skin surface structures with an array of scale types and textures ranging from shark skin denticles with tooth-like structures that protrude above the epidermis to the scales of ray-finned fishes that possess an enormous variety of ridges, protrusions, and ornamentation (Fig. 11; Reif, 1985; Wainwright and Lauder, 2018; Whitear, 1970). The textured surfaces of fishes most likely have many functions, but the skin surface almost certainly plays a hydrodynamic role in swimming (Lauder et al., 2016). The most common premise of fish skin research is that the surface ornamentation and mucus layer (on bony fishes) reduce drag forces and the cost of transport. By creating a smooth body surface both pressure and friction drag forces could be reduced. For shark skin denticles, experiments on both pieces of skin and biomimetic 3D printed denticle arrays (Fig. 11), moved in a swimming motion by a robotic controller, have shown that the surface texture can both reduce drag and also increase thrust by altering the structure and strength of vortices generated by the tail (Oeffner and Lauder, 2012; Wen et al., 2014, 2015). Studies of airfoils printed with a shark denticle surface have also shown that lift can be enhanced and drag reduced: increasing the lift: drag ratio that is critical to high-performance wing-like function (Domel et al., 2018). To date, biomimetic fish skin has not been applied to freely-swimming robotic systems, but advances in manufacturing technology in the near future may allow application of biomimetic skin to fish robots in the field and contribute to improved locomotor function.

Understanding the physical biology of aquatic propulsion offers multiple benefits and opportunities. The process of developing mechanical systems helps us to understand the forces and dynamics that fish experience in their daily lives, which itself can aid in prioritizing conservation actions. At the same time, though, humans also benefit, potentially developing machines that can traverse challenging environments for a variety of applications such as inspecting infrastructure in hazardous environments.

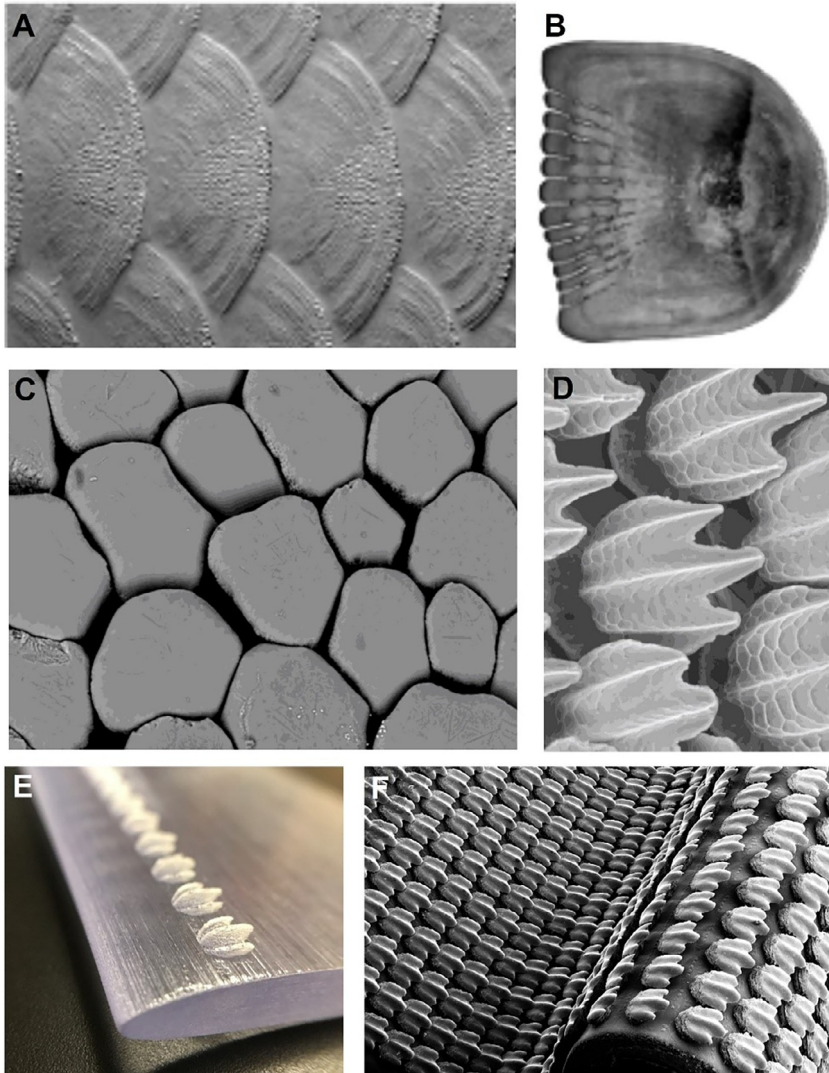


FIG. 11 Fish skin surfaces and biomimetic models. (A) Body surface scales of a bluegill sunfish (*Lepomis macrochirus*) and an isolated ctenoid scale (B; [Lauder et al., 2016](#)). (C) Nose denticles from a smooth dogfish shark, (*Mustelus canis*; [Ankhelyi et al., 2018](#)), and lateral body denticles (D) covering the skin of a bonnethead shark (*Sphyrna tiburo*; [Oeffner and Lauder, 2012](#)). Biomimetic 3D-printed shark denticles attached to the leading edge of an airfoil (E) both improve lift and reduce drag ([Domel et al., 2018](#)), while testing a flexible membrane printed with an array of 3D-printed shark denticles (F) improved swimming performance ([Wen et al., 2014](#)).

Despite progress over the last 15 years in the development of a variety of fish-like robotic systems, swimming performance still lags far behind that of fishes, and there are several areas in particular where improvements could be achieved. Better implementation of swimming kinematics derived from

fishes would likely result in improved swimming speed and maneuverability, as would better streamlining and use of more fish-like body shapes. Robotic systems are often programmed with wave-like movements to generate body undulation without reference to published data on fish kinematics. Many fish species employ very similar body wave motions (Lauder, 2006; Lauder and Tytell, 2006;) which can be implemented into robotic systems to improve swimming performance. Autonomy is a more challenging problem as both power consumption by the robot and communication with a remote controller are difficult problems to solve in underwater locomotion, but improvements in battery technology, artificial intelligence, and machine learning promise to greatly extend the range and autonomy of future fish-like robots.

6.2 Technology for fish conservation biology

Although there are many limitations to current free-swimming fish robotic technology, there are a number of other technological developments that are now being employed to provide insight into fish biology and aid in conservation that are complementary to ongoing robotic research. As mentioned above, drones and airplane tracking are being used to observe and quantify migrating fish populations. In shallow clear waters, aerial observation platforms allow measurement of fish swimming kinematics and speeds, and inter-individual spacing and arrangement that avoids the difficulties of attempting to monitor these variables underwater. For example, Kajiura and Tellman (2016) and Porter et al. (2020) have used drones and an airplane to track blacktip shark movements (*Carcharhinus limbatus*) in clear shallows off the Florida coast.

Second, AUV (autonomous underwater vehicle) and ROV (remote underwater vehicle) technology is being used to better understand the physical environment of fishes and to conduct surveys of fish populations (Stoner et al., 2008; Sward et al., 2019). Recent AUV and ROV deployments in the deep sea have led to remarkable discoveries of fish behavior and occurrence: there is no substitute for visual observation and video recordings which are invaluable for documenting novel behaviors (Lundsten et al., 2009; Reisenbichler et al., 2016). Using currently available technology, considerable progress can be made in understanding fish behavior in the field while ongoing development needed to obtain deployable fish-like robots occurs (Bo et al., 2014; Love et al., 2020).

Third, rapid increases in the development of electronic tags have tremendously expanded our knowledge of fish behavior and been largely responsible for the explosion of studies in the field of movement ecology. The challenges of following fish with mechanical devices can be avoided by simply attaching a tracking system to the fish itself. Tags range from relatively simple passive integrated transponder (PIT) tags (Castro-Santos et al., 1996; Mahapatra et al., 2001; Saboret et al., 2021) to increasingly sophisticated tags that report depth, temperature, body position, and motion using inertial measurement units

(IMUs), often with onboard video cameras that provide direct evidence of behavioral interactions and body motion (Block, 2005; Gleiss et al., 2019; Kohler and Turner, 2001).

Finally, future developments in machine vision and image processing will likely enable automated identification and assessment of fish species and movements when sensors are deployed in marine and freshwater habitats. Using pre-programmed three-dimensional data on a diversity of fish shapes and swimming kinematics, it should be possible to develop automatic vision-based screening methods that can discriminate among species at fish counting fences or selective barriers.

In combination with rapid development of the many different technological systems that will enhance our understanding of fish behavior, better understanding of the physical environments in which fish live and the development of new high-performance fish-like robots, when available, promise to greatly expand our understanding of fish biology and knowledge of how fish respond to human-designed systems like trawls, nets, and passage barriers. In the near future, new robotic systems will enable us to “swim with the fishes” and directly observe how fish respond to, associate with, and avoid both natural and artificial components of their environment.

7 Conclusions

The Anthropocene is a time of unprecedented change. These changes have been particularly acute in aquatic environments. Freshwater biodiversity is seriously imperiled (Dudgeon et al., 2006; Reid et al., 2019), and biomass of marine fisheries is at a fraction of what it was just a century ago (Christensen et al., 2014; Pauly et al., 2002). The ability of fish to move will influence their ability to adapt to these changes, and our understanding of both their abilities and limits will profoundly influence the development of effective management solutions. Technological innovations continue to offer improvements in our ability to understand the ecology, physiology, and behavior of fishes, and how these things interact with a changing environment. In the process of developing these advances, we are also learning more about what the natural world has to teach us, and this is particularly true of understanding how fish move through their environment. Some of that information will inform improved management, but in other cases we see advances in technology that are entirely independent of conservation interests. As we navigate this new age, the ability to move through this evolving environment will determine the outcomes for fish populations and humans alike.

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