REVIEW PAPER

An energetics–performance framework for wild fishes

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Abstract

There is growing evidence that bioenergetics can explain relationships between environmental conditions and fish behaviour, distribution and fitness. Fish energetic needs increase predictably with water temperature, but metabolic performance (*i.e.*, aerobic scope) exhibits varied relationships, and there is debate about its role in shaping fish ecology. Here we present an energetics–performance framework, which posits that ecological context determines whether energy expenditure or metabolic performance influence fish behaviour and fitness. From this framework, we present testable predictions about how temperature-driven variability in energetic demands and metabolic performance interact with ecological conditions to influence fish behaviour, distribution and fitness. Specifically, factors such as prey availability and the spatial distributions of prey and predators may alter fish temperature selection relative to metabolic and energetic optima. Furthermore, metabolic flexibility is a key determinant of how fish will respond to changing conditions, such as those predicted with climate change. With few exceptions, these predictions have rarely been tested in the wild due partly to difficulties in remotely measuring aspects of fish energetics. However, with recent advances in technology and measurement techniques, we now have a better capacity to measure bioenergetics parameters in the wild. Testing these predictions will provide a more mechanistic understanding of how ecological factors affect fish fitness and population dynamics, advancing our knowledge of how species and ecosystems will respond to rapidly changing environments.

KEYWORDS
behaviour, bioenergetics, conservation, ecology, ectotherms, metabolism, physiology

1 | INTRODUCTION: ECOLOGICAL ENERGETICS OF WILD FISH

Energy is the 'fire of life' (Kleiber, 1961) and the key currency that cycles through ecosystems, controlling organismal characteristics including growth and survival, scaling upward to population and ecosystem dynamics (Brown *et al.*, 2004; Tomlinson *et al.*, 2014). At the individual level, bioenergetics can be characterized with an energy-balance equation: *consumption = metabolism + waste +- growth* (Brett & Groves, 1979; Winberg, 1956). Ultimately, animals

must acquire energy (*consumption*) faster than they expend it (*metabolism*) to allocate net resources to growth and reproduction (*growth*), which is essential for biological fitness. However, ecosystems are a complex mosaic of energetic costs and gains that have a major influence on energetic trade-offs, organism behaviour, fitness, distribution and life-history traits (Tomlinson *et al.*, 2014).

Fish bioenergetics have a complex relationship with environmental temperature that has a profound effect on their ecology. Metabolic rate is the rate of energy expenditure (EE, commonly estimated *via* oxygen consumption rate, $\dot{M}_{O2}$; Nelson, 2016), comprising energetic
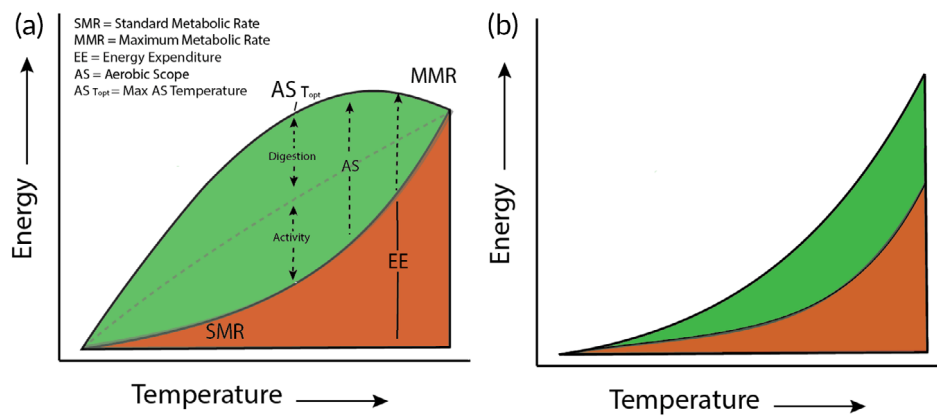
FIGURE 1 Conceptualized relationship between environmental temperature and fish energy expenditure (red), where the minimum is determined by the standard metabolic rate (SMR), and aerobic scope (green), which is the difference between the maximum metabolic rate (MMR) and the SMR. Aerobic scope (AS) may be used for activity and/or digestion (separated by a dashed line), both of which are typically required for energy acquisition. AS T_{opt} refers to the temperature of maximum aerobic scope. (a) and (b) represent generalized forms of two common relationships observed in fish

needs for baseline metabolic maintenance, plus active metabolism allocated to activity and digestion. Most fish are ectotherms, and their metabolic rate increases predictably with environmental temperature (Fry, 1947; Brett, 1964, 1969; Clarke & Johnston, 1999; Figure 1). Fish can also allocate a substantial proportion of their energy budget to activity (Boisclair & Leggett, 1989) and digestion, which is measured as specific dynamic action (SDA; Beamish, 1974; Secor, 2009). The majority of their energy is mobilized with oxygen through aerobic metabolism, the capacity for which also varies dramatically with environmental conditions. This is because fish also have a maximum metabolic rate (MMR) that can be physiologically attained, above baseline metabolic costs (measured as standard metabolic rate, SMR). The difference between SMR and MMR is referred to as aerobic scope (AS), defined as the aerobic metabolic capacity of animals above their basic metabolic needs. Empirical studies have shown that the AS of fish shows two predominant relationships with water temperature, either peaking at intermediate values and declining toward lower and upper extremes (Brownscombe et al., 2017b; Chabot et al., 2016; Eliason et al., 2011; Gillooly et al., 2017; Pörtner, 2001; Pörtner et al., 2017) (Figure 1a) or increasing continually to upper thermal limits (Clark et al., 2011, 2013; Jutfelt et al., 2018; Norin et al., 2014; Raby et al., 2016) (Figure 1b).

Aerobic metabolism fuels most of the life processes of fish and therefore, with few exceptions, at least some minimum level of AS is necessary for locomotion to search for and obtain food, and for incorporating that energy through digestion (Beamish, 1974; Brett, 1964; Clark et al., 2013; Fry, 1947; Gillooly et al., 2017; Jobling, 1995). However, the extent to which AS is relevant to fish ecology is subject to ongoing debate (Clark et al., 2013; Jutfelt et al., 2018; Pörtner et al., 2017). The importance of AS has been demonstrated in diverse ecological contexts across many species (Brownscombe et al., 2017b; Claireaux & Lefrançois, 2007; Clark et al., 2011; Eliason et al., 2011; Gillooly et al., 2017; Jutfelt et al., 2018; Pörtner, 2001; Pörtner & Knust, 2007; Price et al., 2012). For example,

AS varies systematically in sockeye salmon (Oncorhynchus nerka) populations in relation to population-specific migration difficulty associated with the thermal conditions of spawning streams, suggesting it is an important factor in migration success (Eliason et al., 2011; Farrell et al., 2008). Indeed, Burnett et al. (2014) found that the capacity of Pacific salmon to pass challenging water flows using aerobic metabolism (rather than dependence on anaerobiosis) was a strong predictor of their survival to spawning grounds. Furthermore, rates of food consumption tend to relate to AS, with both declining at thermal extremes (Jobling, 1995). Bonefish (Albula vulpes) have been documented to forage on nearshore flats selectively in relation to their optimal (near-maximum) AS (Brownscombe et al., 2017b). Fishes may even behaviourally limit their energy intake (i.e., feeding and subsequent digestion) to retain AS that may be needed in the near future for activities such as locomotion or overcoming a stressor (Jutfelt et al., 2021). Fish that are digesting can also have reduced swimming capabilities (Zhang et al., 2012). In a synthesis of nine tropical and temperate fish species, Payne et al. (2016) found that fish often occupied relatively high water temperatures in their environment, where AS was high but upper lethal limits were avoided. Similarly, Duncan et al. (2020) found that a combination of temperature and oxygen availability appears to constrain the geographic distribution of Roman seabream (Chrysoblephus laticeps) based on their aerobic metabolism.

Despite empirical support for the role AS plays in fish ecology, it is not a universal predictor of behaviour and fitness. For example, in contrast to the findings of Eliason et al. (2011), other Pacific salmon species and populations had thermal performance curves for AS that did not align with the historically experienced thermal regimes (Clark et al., 2011; MacNutt et al., 2006; Raby et al., 2016). Norin et al. (2014) also found that AS for barramundi (Lates calcarifer) increased to upper lethal limits, and fish behaviourally selected cooler temperatures than those at which AS was maximized. In Atlantic halibut (Hippoglossus hippoglossus) fed to satiation, growth peaked at intermediate temperatures whereas AS continued to increase throughout the ecologically

relevant temperature range of the species (Gräns *et al.*, 2014). Indeed, conversion efficiencies from food to net somatic growth can vary widely with temperature (*e.g.*, Fitzgibbon *et al.*, 2017; Martinez-Palacios *et al.*, 1990) and meal size (Norin & Clark, 2017). Optimal efficiencies do not necessarily coincide with maximum AS even when food is unlimited (Khan *et al.*, 2014). This could be related to other physiological processes (*e.g.*, digestive enzyme activity; Schulte, 2015) whose performance may not be tightly controlled by oxygen supply. The reality that not all performance metrics will align at the same optimal temperature was given the label of 'multiple performances – multiple optima' by Clark *et al.* (2013) in their critique of AS as a unifying metric of animal performance. Consistent with this concept is the hypothesis that some fish species are 'oxygen-independent', meaning their thermal tolerances (and perhaps optima) are not linked with capacity for oxygen supply (Ern, 2019; Ern *et al.*, 2016).

Overall, the body of scientific evidence suggests that there are some aspects of the lives of (oxygen-dependent) fish where AS is highly relevant as a measure of physiological performance, such as exercising to navigate challenging water flows (Burnett *et al.*, 2014) or when foraging, which presents combined metabolic demands for exercise and digestion (Brownscombe *et al.*, 2017b; Jutfelt *et al.*, 2020). However, some species may be less limited by oxygen supply and/or driven by other optima (Clark *et al.*, 2013; Ern *et al.*, 2016). Furthermore, the capacity of fish to achieve net energy gain ultimately determines their growth, an important aspect of biological fitness, therefore, in some contexts, energy conservation may be more relevant. For example, during an energetically demanding parental care period, reduction of EE to conserve energy stores and avoid starvation may be more important to fitness than maximizing AS (Brownscombe *et al.*, 2017a). In another example, Lear *et al.* (2020) found that extended high water temperatures during a summer drought season can result in massive energetic costs that threaten fish survival and fitness. Furthermore, in the wild, fish are presented with a variety of challenges, such as navigating water flows to minimize energetic costs (McElroy *et al.*, 2012), avoiding predators (Gallagher *et al.*, 2017) and finding food (Persson, 1986). Thus, a variety of factors could influence fish behaviour, thermal experience and fitness beyond what may be optimal for their energetics.

Although bioenergetics clearly plays an important role in the lives of all animals, the exact roles of EE and AS in shaping behaviour and fitness in wild fish are not yet clear. Based on the growing body of fish energetics research discussed above, we present an energetics–performance framework that posits that EE or AS drive fish behaviour and fitness depending on the ecological context. Within this framework, we present four testable predictions related to how fish behaviour and fitness may relate to ecological conditions including interactions between EE, AS, food availability, predator and prey spatial distributions, and metabolic flexibility. Although this is not an extensive list of the factors that could influence these relationships, the empirical evidence discussed above supports that these may be predominant factors that influence the relevance of EE and AS in fish ecology. The predictions we describe are not novel individually, and many of them make connections to previous empirical or conceptual

papers. For example, the recently proposed 'aerobic scope protection hypothesis' emphasizes the way in which the temperature-dependence of SDA can cause fish to reduce feeding at high temperatures to preserve AS (Jutfelt *et al.*, 2021). By integrating existing hypotheses about bioenergetics and metabolism, our motivation here is to explore potential overarching mechanisms that explain fish behaviour, distribution and fitness in the wild. Building on a strong foundational knowledge of fish metabolism and bioenergetics (*e.g.*, Brett & Groves, 1979; Jobling, 1995; Tytler & Calow, 1985; Winberg, 1956), we consider how EE, AS and ecological conditions may interact dynamically over space and time. For example, we consider the dynamic nature of food availability and environmental temperature in the wild, including the fact that fish can often behaviourally thermoregulate. In addition to describing these predictions in more detail below, we provide a conceptual example that illustrates how these factors might combine to influence spatial–temporal patterns of wild fish movement and habitat use, and then conclude with some potential approaches to collect relevant data.

2 | ENERGETICS–PERFORMANCE PREDICTIONS

2.1 | Resource availability

The core prediction within the energetics–performance framework proposed here is that ectothermic fish alternate between states of energy conservation and aerobic performance depending on resource availability (Figure 2a). Specifically, when food availability is high, fish will select temperatures that enable near-maximum AS to facilitate maximum rates of energy acquisition during a time when aerobic metabolism is required for exercise to capture/acquire prey, as well as digestion (Brownscombe *et al.*, 2017b; Jutfelt *et al.*, 2020; Persson, 1986). Notably, fish may not select temperatures corresponding *exactly* to absolute maximum AS, but those close to it, perhaps roughly within the bounds of pejus temperatures (*i.e.*, onset of capacity limitations and hypoxemia; Pörtner *et al.*, 2017). Conversely, when resource availability is more limited, fish would be expected to select for lower temperatures to minimize routine EE (Figure 2a). There is evidence that food deprivation can result in fish selecting colder water as a potential energy conservation mechanism (Sogard & Olla, 1996). Moreover, fish may enter energy conservation states for reasons independent of environmental resource availability, where their physiology constrains feeding. Such is the case for migrating salmon (Groot, 2010) and nest guarding male largemouth bass (Hanson & Cooke, 2009). Environmental factors may also cause an energy conservation state by limiting AS, such as in warmwater fishes in temperate regions at cold temperatures during winter (Oliver *et al.*, 1979).

It is notable that fish may not be in a physiological state consistent with maximal energy acquisition, even if food availability is high. This may be particularly relevant to short-term laboratory studies, where fish are placed in novel environments and often experience higher levels of stress from holding, handling and experimentation. It stands that exposing fish to water temperatures that correspond to
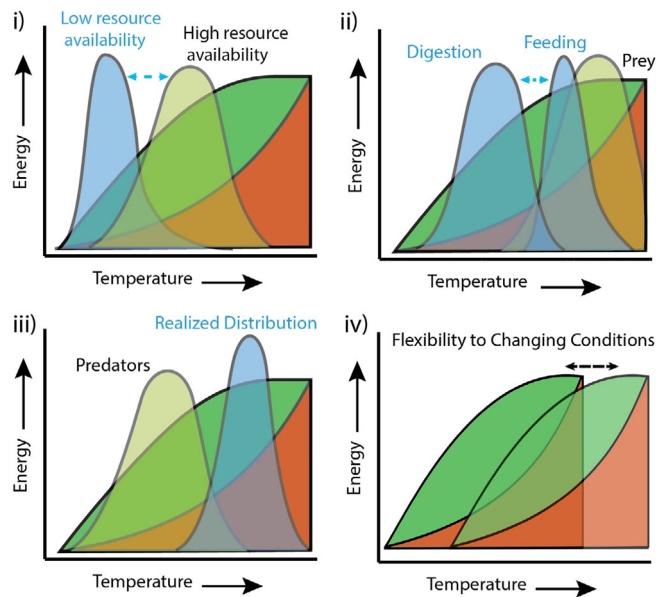
FIGURE 2 Conceptualized relationship between environmental temperature and energetic costs (red), the minimum of which is determined by the standard metabolic rate (SMR), and aerobic scope (green), illustrating (i) resource availability, (ii) prey shift, (iii) predator shift and (iv) flexibility–resiliency predictions. Yellow and blue areas represent the predicted density distribution of temperature use by the focal fish, their prey or predators

maximal AS often does not result in maximal growth in long term holding experiments (*e.g.*, Fitzgibbon *et al.*, 2017; Martinez-Palacios *et al.*, 1990), and other optima may drive net energy acquisition such as digestive efficiency. Regardless of the physiological or biochemical mechanism, this can be framed in energetics, where reduced digestive efficiency results from the ratio of energetic costs to gains. It could be that growth efficiency is reduced at maximal AS because routine energetic costs outweigh simultaneously high rates of energy assimilation, reducing net energy gain.

Compared to controlled laboratory studies, thermal ecology is far more complex for wild fish, with variance in temperature availability over space and time, enabling a wide range of potential selection patterns and strategies. For example, Sims *et al.* (2006) found that dogfish (*Scyliorhinus canicula*) 'hunt warm, rest cool', exploiting warm water prey while reducing overall energetics costs. This highlights that wild fish can exploit a range of conditions that may correspond to multiple optima related to metabolic performance and energy conservation, and further reinforces that laboratory studies are indeed major simplifications of wild fish energetics, where studies on temperature selection and physiological factors require serious consideration of ecological context for design and interpretation.

2.2 | Prey shift

As discussed above, there is evidence that temperature can influence fish foraging behaviour, where fish selectively forage at water temperatures consistent with metabolic performance (Brownscombe

et al., 2017b; Persson, 1986). Indeed, AS may be most relevant in foraging contexts because of the high metabolic demands from the combination of exercise and digestion (Jutfelt *et al.*, 2021). However, in dynamic natural ecosystems, there may be cases where a fish's prey are not located in thermally optimal habitat. Therefore, the *prey shift* prediction states that prey distribution may cause fish to forage at water temperatures that are sub- or supra-optimal for AS and/or EE (Figure 2b). This may be consistent with the observation by Sims *et al.* (2006) that dogfish 'hunt warm, rest cool', but the temperature–AS relationship is not known for that species. In another example, in tropical tidal creeks of the Bahamas, bonefish forage in shallow upper tidal creeks that are thermally dynamic. For short periods, bonefish may occupy waters >35°C, at which AS is less than one-third of the peak AS value that occurs at 27°C (Murchie *et al.*, 2011, 2013; Nowell *et al.*, 2015). This is an example where bonefish enter drastically warmer water, where energetic costs are high and AS is low, for a short period to exploit available prey. In dynamic and rapidly changing aquatic ecosystems, fish may simply have to go where their food is, even if it means occupying temperatures that do not optimize performance.

2.3 | Predator shift

Predation is a major driving factor in animal ecology due to its direct influence on prey fitness, and it is well established that animals are often confronted with competing demands of foraging and predator avoidance (Hugie & Dill, 1994; Lima & Dill, 1990; Lind & Cresswell, 2005; Milinski & Heller, 1978; Werner *et al.*, 1983). Indeed, the landscape of fear concept supports that even a perceived predation risk due to the presence of predators can have a major influence on animal behaviour in the wild (Laundre *et al.*, 2014). Gallagher *et al.* (2017) provide some direct discussion on how fear of predators can affect behaviour in ways that overwhelm the effects of bioenergetic trade-offs. Therefore, the *predator shift* prediction states that predators can cause fish to shift their thermal habitat selection away from optimal AS and/or EE to reduce risk of predation (Figure 2c). There is a strong basis to support the suggestion that predation pressure can drive the movement patterns of prey species, which likely applies to ecological energetics as well.

Overall, the purpose of reviewing the *prey shift* and *predator shift* predictions presented here was not to provide a comprehensive description of how these factors may drive fish energetics or the broad set of factors that may do so, but rather to identify some key factors that may influence the relevance of energetic costs and metabolic performance to fish fitness, and also cause fish to shift away from what would otherwise be considered bioenergetically optimal in natural ecosystems. Indeed, factors such as competition (which affects food availability) and predators are recognized as disruptors of environmental–organismal relationships (Grober-Dunsmore *et al.*, 2009). Another major component to fitness is reproduction, which is not covered here, but may also be an important source for discrepancy in relationships between fish behaviour and optimal bioenergetics.

2.4 | Flexibility–resiliency

In the face of rapid environmental change, including climate change, animal behavioural and physiological flexibility is considered to be a major factor that will ultimately determine individual and population level responses (Gienapp *et al.*, 2008; Naya *et al.*, 2011; Sih, 2013). The *flexibility–resiliency* prediction posits that metabolic flexibility, both phenotypically and evolutionarily, will be a major determining factor in how fish will respond to changing environmental conditions (Figure 2d). There is a particular concern that increasing water temperatures (amongst other factors, including increased CO_2 in oceans) will cause temperatures to shift away from metabolic optima for many fish species (Farrell *et al.*, 2008; Rummer *et al.*, 2014). For example, Rummer *et al.* (2014) found that six tropical fish species are living at or just above their optimal AS and maximum MMR, leading to concern for such species under climate change scenarios. Indeed, tropical fishes typically occupy more stable conditions, and hence their thermal tolerances are typically narrower than those of their temperate counterparts. However, fish EE and AS can also be highly flexible phenotypically. For example, Norin *et al.* (2014) found that barramundi AS was higher during acute exposure to 38°C than at an acclimation temperature of 29°C, and after acclimation to 38°C AS was similar to that at 29°C. In the same species and temperature range, Scheuffele *et al.* (2021) found that AS was flexible amongst acclimation temperatures in amplitude but not in breadth, that is, AS was generally higher at the acclimation temperature, but did not increase amongst other tested temperatures or due to exposure to a variable temperature regime. Many studies have also identified variation in fish SMR due to food availability, which results in differences in growth responses amongst individuals (Auer *et al.*, 2020; Guppy & Withers, 1999; Van Leeuwen *et al.*, 2012). Metabolic rate is also heritable and can evolve rapidly, often with a close relation to life-history traits (Auer *et al.*, 2018). Overall, there is high potential for both phenotypic and genotypic variation in fish metabolic traits, and therefore there is a need to consider long-term flexibility in the context of climate change. However, the timescale of climate warming (*i.e.*, years to decades) is challenging to assess with experimental studies and requires consideration of phenotypic flexibility as well as multigenerational evolutionary adaptation. As highlighted in the examples above, the exact nature of how metabolic metrics may change over time within individuals and across generations is likely to be complex, and the example shown (Figure 2d), with a simple shift in SMR and MMR with temperature, is meant to be illustrative and not an exact prediction of how all species may respond.

The flexibility–resiliency prediction is also highly relevant to other predictions within the framework. For example, if predators consistently force prey into alternative water temperatures, the prey may adapt to their realized thermal regime. It is also broadly relevant for study design and interpretation. For example, if a given fish species/population is highly flexible metabolically (*i.e.*, their EE and AS vary over time due to factors such as acclimation temperature or physiological state), there is a risk that short-term laboratory or field studies may fail to capture an accurate representation of longer-term

ecological energetics. In assessing the potential effects of environmental changes such as those associated with climate change, it is also important to consider that behavioural adaptation is another a key determinant of fish responses as in some cases (*e.g.*, open oceans) species may be able to expand their range or alter temporal patterns of space use to maintain life in similar conditions (Carroll *et al.*, 2021), while in others (*e.g.*, isolated lakes) physiological adaptations will be required.

3 | CONCEPTUAL EXAMPLE

To illustrate the energetics–performance framework in a spatially explicit example, we demonstrate how environmental conditions such as water temperature and prey availability could influence the potential energetic costs and gains for foraging in fish (Figure 3). This hypothetical example illustrates the *prey shift* prediction where the shallow nearshore intertidal zone has high prey availability, but also the warmest water temperatures (32°C) at this time period, causing the foraging fish to have limited AS for activity and digestion, and high EE. Fish may forage in this location only for short periods of time until AS is occupied by digestion (Zhang *et al.*, 2012), hindering further foraging. In addition, higher EE in warm shallow habitats makes them costlier to inhabit if food intake is not considered. In the intermediate nearshore area, temperatures are relatively moderate in this example (27°C), enabling higher AS and lower EE, which may make it an optimal foraging location despite lower prey availability. If fish are not foraging for a range of potential reasons (*e.g.*, predators or thermal exclusion from the foraging habitat), they would be expected to occupy areas further offshore in relatively cool water (22°C) where both AS and EE are moderate and food availability is lower. In reality, these focal fish are likely to move amongst these habitats frequently, with foraging opportunities being a dominant factor. For example, fish may choose to save energy by occupying cooler offshore waters during the daytime and forage more actively at night when they may be more energetically efficient at prey capture (*i.e.*, lower activity costs per kilojoule of food intake). Indeed, energy spent on activity can be a substantial and worthwhile investment when it translates into food intake, but higher activity costs would result in lower growth rates if all other factors are held constant (food intake, temperature, *etc.*; Rennie *et al.*, 2005).

4 | CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

Bioenergetics is a powerful approach to characterize organisms and ecosystems (Tomlinson *et al.*, 2014), especially with a focus on energy mobilization through metabolism (Brown *et al.*, 2004). As aquatic ectotherms, fish present an interesting case for energetics studies due to their highly variable metabolic rate (energy expenditure, EE) and metabolic capacity (aerobic scope, AS). However, the role of various metabolic metrics in fish ecology is not clear, especially when it comes to

FIGURE 3 Map of the hypothetical distribution of water temperature, fish and their prey in a coastal marine habitat to illustrate the influence of a water temperature regime on fish energy expenditure (EE) and aerobic scope (AS). The dotted line indicates the mean of a hypothetical range of EE and AS values
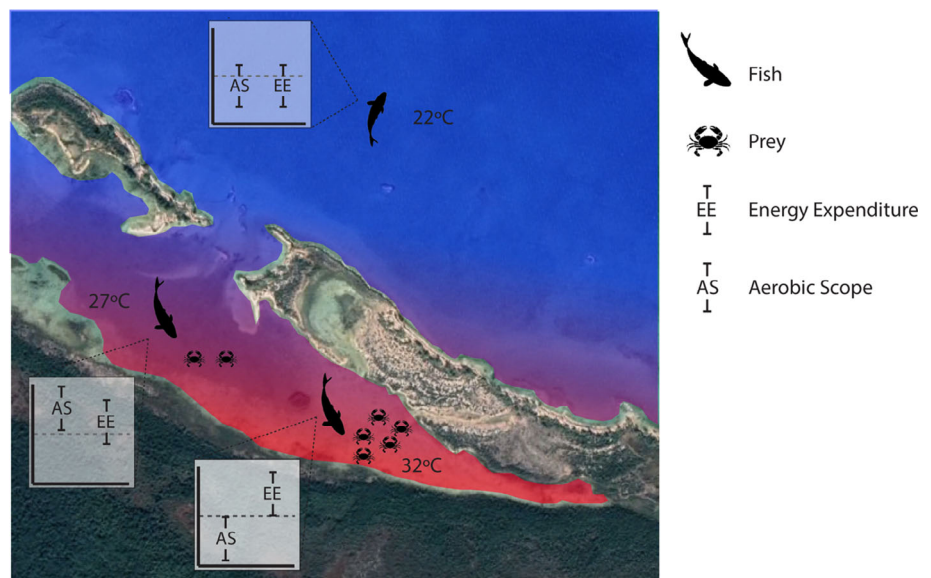
AS (Jutfelt *et al.*, 2018; Pörtner *et al.*, 2017). In attempt to help address these uncertainties, we present an energetics–performance framework that posits that EE or AS affect fish fitness depending on the ecological context, therefore fish may shift along a gradient between prioritizing one or the other. There seem to be some clear cases when AS is of relevance, especially when foraging (Brownscombe *et al.*, 2017a; Jutfelt *et al.*, 2020) or engaging in intense exercise such as during upriver migration (Burnett *et al.*, 2014). At the landscape (aquascape) scale, AS has been identified as a potential factor constraining species distributions in relation to temperature (Duncan *et al.*, 2020; Payne *et al.*, 2016; Ruan *et al.*, 2014). However, in other ecological contexts, such as fasting during parental care or surviving a warm drought season, minimizing EE to conserve stores may be more relevant (Brownscombe *et al.*, 2017a; Hanson & Cooke, 2009; Lear *et al.*, 2020). The energetics–performance predictions presented here attempt to address this, suggesting specific factors that may modulate the ways in which EE or AS drive fish behaviour and fitness. It is important to recognize that in natural ecosystems, fish are faced with dynamic, uncertain conditions as well as trade-offs amongst various factors (*e.g.*, finding prey, avoiding predators, inhabiting optimal temperatures for EE or AS). Animals can use diverse strategies to achieve some level of growth and reproductive fitness (Auer *et al.*, 2018; Gross & Charnov, 1980; Winemiller & Rose, 1992). The stated predictions (Figure 2) aim to address some of these trade-offs, but by no means represent a comprehensive list of the wide range of factors that may drive behaviour and fitness. They do provide a range of potential research avenues addressing key factors (temperature, predation risk and prey availability) that may influence animal energetics over long time scales in the wild. To this end, laboratory studies serve as a key knowledge source, but studies of wild fish are necessary to integrate ecological realism. For example, we suggest that short-term holding experiments are unlikely to provide relevant assessments of temperature selection behaviour in relation to AS because fish are unlikely to be in a physiological state

oriented to energy acquisition. However, laboratory experiments can be used to quantify the thermal dependence of AS, SDA and other parameters in ways that can help interpret fish movement and habitat use in the wild by pairing laboratory experiments with field-based fish tracking studies. Furthermore, the notion that fish species may be categorically oxygen-dependent or oxygen-independent in terms of temperature-related performance (Ern, 2019) is a key avenue for further research that may help to resolve the species and contexts in which common metabolic metrics such as AS are important drivers of fish ecology and fitness.

There is a growing array of tools available for remote measurement of fish bioenergetics, some of the most exciting of which include acceleration and heart rate biologgers, which can generate remote, spatially explicit estimates of various relevant metabolic metrics when calibrated in the laboratory (Cooke *et al.*, 2016). There is a key need for future studies to pair remote metabolic estimates from these sensor tags with simultaneous measurement of relevant environmental conditions such as temperature, as well as prey availability, feeding behaviour and predation risk. There are vast amounts of fish telemetry data accumulating through telemetry networks (Iverson *et al.*, 2019; Udyawer *et al.*, 2018; Young *et al.*, 2020), which should be useful when integrated with available environmental data and laboratory measures of fish bioenergetic metrics. The best wild systems for testing the predictions presented here may be small inland lakes with simple food webs in which full fish-tracking coverage can be achieved, in addition to tracking fish (*e.g.*, location plus body temperature, activity and/or heart rate) across two trophic levels (predators and prey). However, insightful studies are possible across a broad range of systems, especially with long-term data sets (*e.g.*, Carroll *et al.*, 2021). Integrating multiple sample techniques may also be beneficial, for example pairing fish tracking with passive acoustic monitoring to assess the distribution of smaller-bodied fishes. This sort of work would aid in addressing the key balance of energetic costs and gains that drives net energy gain and biological fitness, and generating data

relevant for testing the energetics–performance predictions stated here with real-world data.

AUTHOR CONTRIBUTIONS

All authors contributed to the generation of these ideas and manuscript preparation.

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