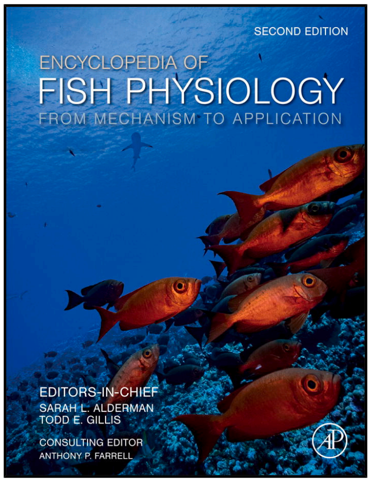

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Temperature and fish biology: Insights from metabolism

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Key points

- Introduce the idea of metabolism as a tool for understanding temperature effects upon fish.
- Provide a primer of common metabolic traits, and how they are measured and interpreted.
- Address how changes in metabolic performance reflect the acclimation or evolutionary history of fishes.
- Provide examples of how temperature-dependent metabolism is being used to explore fish conservation, ecology, and behavior.

Glossary

Absolute Aerobic Scope The difference between an organism's aerobic maximum metabolic rate and its standard metabolic rate.

Acclimate The physiological process by which an organism gradually adjusts its physiological, behavioral, or biochemical traits in response to changes in its environment, such as temperature, humidity, or altitude.

Eurythermal Capable of tolerating a wide range of temperatures without significant negative effects.

Factorial Aerobic Scope The quotient of the maximum metabolic rate divided by the standard metabolic rate.

Hypoxia A condition characterized by an insufficient supply of oxygen to body tissues due to reduced oxygen levels in the environment or impaired oxygen transport within the body.

Intraspecific Aspects which apply within a single species.

Interspecific Aspects which span across multiple species.

Maximum Metabolic Rate The highest metabolic rate an organism can achieve during periods of intense activity or stress.

Poikilotherms Organisms whose body temperature is dependent upon their external environment.

Resting Metabolic Rate The rate at which an organism expends energy while at rest.

Standard Metabolic Rate The metabolic rate of an organism at rest and under specific standardized conditions, often involving a controlled temperature and fasting state.

Stenothermal Capable of tolerating only a narrow range of temperatures.

Nomenclature

AAS Absolute Aerobic Scope
ETO Evolutionary Trade-Off Hypothesis
FAS Factorial Aerobic Scope

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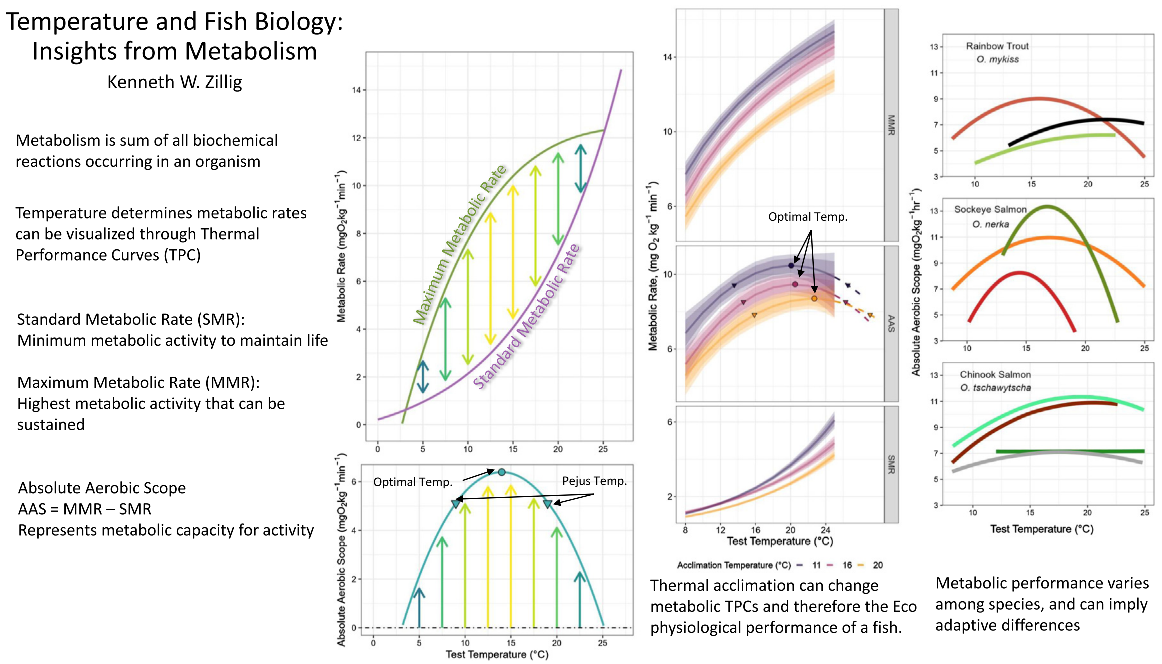
MCA Metabolic Cold Adaptation Hypothesis
MMR Maximum Metabolic Rate
Q_{10} Temperature coefficient
RMR Resting Metabolic Rate
SDA Specific Dynamic Action
SMR Standard Metabolic Rate
T_{CRIT} Upper or lower temperature where the AAS TPC is equal to zero. Theoretically defines the upper and lower temperatures for organism survival
T_{OPT} Temperature at which the maximum AAS is achieved
TPC Thermal Performance Curve
T_{PEJ} Temperature at which AAS TPC is reduced past a threshold, commonly 50 or 90% of maximum
U_{CRIT} Maximum Sustained Swim Speed
UTD Universal Temperature Dependence Hypothesis
ϕ Metabolic Index

Abstract

Fish are found in nearly every marine and freshwater ecosystem on planet Earth, and therefore contend with a wide range of environmental temperatures. Temperature is a fundamental environmental variable underpinning physiology, particularly for pokilothermic organisms (such as fish). Therefore, a fish's response to temperature is an integration of thermal effects ranging in scale from the molecular to the whole organism. This article uses metabolism as a lens to understand the impact of temperature on the physiology and ecology of fishes. Metabolism encompasses all the biochemical processes necessary to life, and therefore can provide insight into the influence of environmental temperature. Metabolic research focuses on specific rates of activity (e.g., Standard Metabolic Rate, Maximum Metabolic Rate, Aerobic Scope). Metabolic research has revealed phenotypic acclimation to environmental change and physiological adaptation of fish to their thermal environment. Thereby, the study of metabolism enables understanding of environmental stressors, drivers of adaptation and implications of interspecies variation. Finally, understanding the metabolic response of fish to temperature change is empowering researchers to better understand and predict the effects of climate change on aquatic and marine ecosystems.

Teaching slide



Temperature and Fish Biology:
Insights from Metabolism

Kenneth W. Zillig

Metabolism is sum of all biochemical reactions occurring in an organism

Temperature determines metabolic rates can be visualized through Thermal Performance Curves (TPC)

Standard Metabolic Rate (SMR):
Minimum metabolic activity to maintain life

Maximum Metabolic Rate (MMR):
Highest metabolic activity that can be sustained

Absolute Aerobic Scope
AAS = MMR – SMR
Represents metabolic capacity for activity

Thermal acclimation can change metabolic TPCs and therefore the Eco physiological performance of a fish.

Metabolic performance varies among species, and can imply adaptive differences

Introduction

Fish represent the largest group of vertebrate taxa and are found in nearly every marine and freshwater ecosystem on planet Earth. They can withstand a wide variety of thermal conditions ranging from −2.5 °C to 44 °C. As poikilothermic ectotherms (with some exceptions) the body temperature of a fish is dependent on that of the surrounding water, and therefore reflects the breadth and dynamism of thermal conditions on daily, annual, and even decadal timescales. Fish, as a taxa, respond to temperature through diverse strategies ranging from evolutionary adaptations to fine behavioral changes. Therefore, understanding how the physiology of fishes is influenced by temperature across spatial and temporal scales is relevant to predicting species' responses to climate change, determining the impacts of anthropogenic actions, and illuminating the diverse biology represented by fishes around the world.

Metabolism is a lens through which scientists have gained remarkable insight about the effects of temperature on fish behavior, ecology, and physiology. An animals metabolism captures the sum of biochemical processes that produce or consume energy needed to maintain homeostasis, generate somatic growth, and complete development. As ectotherms, fish metabolism is predominantly influenced by environmental temperature, and therefore understanding the influence of temperature on metabolism can lead to understanding thermal effects throughout fish biology. Metabolic processes require the acquisition of energetic fuels and the excretion of waste products, as well as the acquisition and transportation of oxygen. The energy produced through metabolism supports all of a fish's activities both internal and external such as fish movement or growth. The fundamental nature of metabolism makes the study of thermal effects upon metabolic processes a foundational component of understanding and predicting the effect of temperature on fish physiology, behavior, and ecology. Therefore, by investigating the effects of temperature on metabolic pathways as well as measures of whole organism performance (e.g., growth, developmental rates) we gain insight into the integrative effects of temperature across the organism.

Technological advancements have rapidly improved our ability to measure fish metabolism and correspondingly the research questions and real-world applications of metabolic research have expanded in recent decades. This proliferation of metabolic research has opened new hypotheses about the thermal limits of fishes, new methodologies for assessing thermal suitability, and a new understanding of how fish have evolved to tolerate and thrive under a wide variety of thermal conditions.

Metabolism: A primer

Metabolism represents all the chemical processes involved in sustaining life, which can be coarsely divided into two sub-processes; anabolism and catabolism. Anabolism is a constructive process by which energy is expended to synthesize complex molecules from simpler components. For instance, constructing cellular membranes and proteins from simple lipids or amino acids. Catabolism is the opposite, a destructive process of breaking down complex molecules (e.g., glucose) to produce adenosine triphosphate (ATP) which is the chemical currency of energy. Catabolism can occur through two principal pathways; aerobic metabolism, which consumes oxygen, and anaerobic metabolism, which can occur in the absence of oxygen.

Aerobic metabolism is the more efficient catabolic process, producing greater quantities of ATP per glucose molecule (i.e., $C_6H_{12}O_6 + 6\ O_2 \rightarrow 6\ CO_2 + 6\ H_2O + 30{-}36\ \text{ATP}$), and is the preferred metabolic pathway for fishes. Anaerobic metabolism produces less ATP per glucose molecule and yields additional metabolic byproducts (e.g., $C_6H_{12}O_6 \rightarrow 2\ \text{Lactate} + 2\ \text{ATP}$), which can be toxic if not excreted. The vast majority of teleosts, when using anaerobic metabolism will produce lactate as a byproduct, which is toxic and therefore is rapidly converted into lactic acid. However, when common goldfish (*Carassius auratus*) are deprived of oxygen they will produce ethanol as an anaerobic byproduct. Ethanol can be more readily excreted from the body than lactate and provides goldfish the ability to survive the extended hypoxic conditions (4−5 months) common to frozen lakes during wintertime (Fagernes et al., 2017).

Due to the stoichiometric consumption of oxygen (i.e., six oxygen molecules are consumed for every glucose molecule), diverse methods exist for quantifying aerobic metabolism in real-time. Respirometry is the most common approach whereby changes in the oxygen concentration attributable to fish (i.e., oxygen uptake rate) serve as a proxy for aerobic metabolic rate, often represented as milligrams of oxygen (mgO_2) consumed per minute per kilogram of fish ($mgO_2\ min^{-1}\ kg^{-1}$). To measure the rate of oxygen uptake, fish are placed in a small oxygen-impermeable chamber of known volume which can then be sealed (**Fig. 1**A). Accompanying the fish is a fiber-optic probe that reports the oxygen concentration of the water in the chamber. Once the chamber is sealed, the fish absorbs oxygen from the water through its gills, which is then consumed in aerobic metabolic reactions. As oxygen is absorbed by the fish, the oxygen concentration in the water decreases, which is detected by the probe. A metabolic rate is calculated by determining the change in oxygen over time. Fish exhibiting a faster metabolic rate will deplete oxygen in the chamber more quickly than fish that exhibit a slower metabolic rate. To repeatedly measure metabolic rates the respirometry chamber can be unsealed and oxygenated water can be flushed into the chamber prior to resealing the chamber. This process of repeated sealing and unsealing of the chamber to gather multiple measures of metabolic rate is called intermittent respirometry and is the primary method for assessing the aerobic metabolic rate in fishes.

Anaerobic metabolism is less easily measured and real-time quantification remains elusive as the process occurs internally, without the consumption of external reagents (e.g., dissolved oxygen). Post-event sampling of fish tissues may provide evidence of anaerobic activity through concentrations of metabolic byproducts such as lactate or phosphocreatine. An alternative approach to determining anerobic metabolic performance involves placing fish in hypoxic (low oxygen) or anoxic (no oxygen) conditions to isolate anaerobic

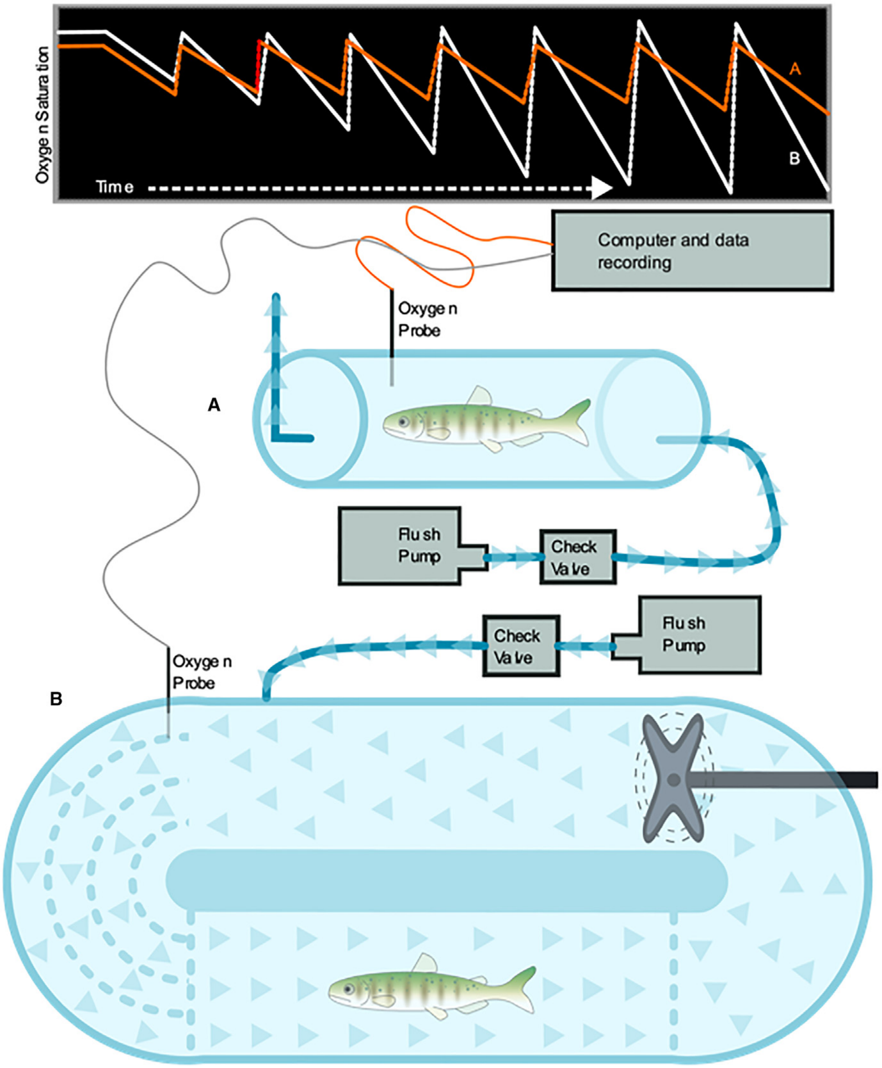


Fig. 1 Diagram of a Static (A) and Swimming (B) Respirometer design. In both designs, fish are contained in a sealed chamber. Fresh water is pumped into the chamber via a flush pump and can be sealed via the check valve when the pump is stopped. An oxygen probe measures the oxygen saturation in each chamber which is plotted throughout time. Dashed line segments represents periods when the flush pump is active, while solid segments capture the consumption of oxygen by the fish when the chambers are sealed. A swimming respirometer forces a fish to swim against a controlled current. If the current is increased, a fish will swim harder and consume more oxygen, represented by the increasing steepness of the solid white lines. Either chamber design may be used to assess standard metabolic rate, while swimming respirometers are commonly used to measure maximum metabolic rate.

metabolism as an organism's only pathway for energy generation. The duration of tolerance to these low or no-oxygen conditions can provide insight into a fish's anaerobic capacity (Hochachka, 1990; Nelson and Lipkey, 2015; Claireaux and Chabot, 2016).

As temperature increases so do the rates of metabolic reactions and the consumption of metabolic reactants (e.g., oxygen for aerobic metabolism). Meeting the demands of a faster metabolism is the requirement of multiple interacting temperature-influenced organismal, cellular, and molecular processes. For example, a fish's heart rate and stroke volume both influence the volume of blood passing through the gills and respiring tissues and subsequently, the capacity of the fish to absorb oxygen from the environment to fuel aerobic performance (Gamperl and Farrell, 2004). As ectotherms, both heart rate and stroke volume are temperature-dependent, with higher temperatures typically leading to faster and more voluminous heartbeats. This temperature-associated increase in cardiac performance can be due to changes in contractile performance of muscle fibers (Gamperl and Syme, 2021), sensitivity of muscle fibers to Ca^{2+} as well as passive properties of the heart (e.g., collagen content) (Keen et al., 2016).

Advances in respirometry technology in the past two decades have greatly increased research on fish metabolism across a range of environmental conditions (e.g., temperature, salinity), developmental stage (e.g., embryo, larvae, juvenile, adult), and organismal state (e.g., swimming vs. resting, healthy vs. diseased). This has allowed for a better understanding of how environmental conditions influence fish metabolism. For example, collecting metabolic data across a range of temperature exposures can produce a Thermal Performance Curve (TPC) which provides insight into how a fish's metabolic rates and capacity change with changes in the thermal environment (Schulte et al., 2011). TPCs typically have a curvilinear shape across a range of temperatures. As temperatures increase, metabolic rates typically rise until they reach an optimum temperature (T_{OPT}) at which metabolic rate or capacity are maximized. As temperatures increase further, metabolic rates and capacity begin to decline, sometimes precipitously. It is important to note that while a bell-curve shape is typical of TPCs, there can be great variation depending on the species and the physiological trait being measured. TPCs can be useful in identifying critical temperatures (T_{CRIT}) where temperature conditions are not conducive to organisms' survival, thermal optima (T_{OPT}) where thermal conditions support the greatest performance, and pejus temperatures (T_{PEJ}) where metabolic performance begins to decline (**Fig. 2**).

Metabolic research has led to the development of two major hypotheses that attempt to address the thermal constraints on fish physiology; the Oxygen-and-Capacity Limited Thermal Tolerance (OCLTT) hypothesis and the Temperature Dependency of Electrical Excitability (TDEE). The OCLTT hypothesis states that a fish's thermal limits are determined by its inability to meet the oxygen demands of its tissues (Pörtner and Knust, 2007; Pörtner and Farrell, 2008). An indicator of limited oxygen delivery is a reduced aerobic metabolic capacity. Limited oxygen-delivering capacity has multiple proposed mechanisms including changes in circulation, efficacy of oxygen absorption, and the temperature-dependency of kinematic reactions. Support for the OCLTT hypothesis is mixed, with some species adhering well to the expectations of the hypothesis and others not. For example, the metabolic performance of eight populations of adult sockeye Salmon (*Oncorhynchus nerka*) from the Fraser River exhibited declining metabolic capacity associated with extreme temperatures, and T_{OPT} was associated with temperatures commonly encountered in the wild (Eliason et al., 2011). However, other studies have not found clear associations between the loss of aerobic metabolic performance and thermal limits. For instance, work on Barramundi (*Lates calcarifer*) found that T_{OPT} was attained at temperatures approaching T_{CRIT} (Norin et al., 2013). Likewise, juvenile Chinook salmon (*O. tshawytscha*) exhibited near-maximal metabolic capacity at temperatures just below lethality (Zillig et al., 2023a,b). A meta-analysis of metabolic rates from marine poikilotherms found that only 42% (31 of 73 datasets) identified clear estimates of T_{OPT}, while the remaining studies found that metabolic rates did not decline at temperatures approaching T_{CRIT} (Lefevre, 2016). In these instances, there was not an observed decline in metabolic capacity associated with high temperature, violating a prediction of the OCLTT.

An alternative hypothesis is the Temperature Dependency in Electrical Excitability (TDEE), which posits that within excitable cells (e.g., cardiac cells) Na^+ and K^+ ion gates become disorganized at extreme temperatures. This disrupts the electrical potential generated by these cells and their ability to generate an action potential is compromised, preventing normal cardiac function and ultimately death (Vornanen, 2016). This hypothesis is supported by work on brown trout (*Salmo trutta*) and rainbow trout (*O. mykiss*), which found that heart rate declined at high temperatures due to changes in cardiac excitability (Vornanen et al., 2014; Haverinen and Vornanen, 2020).

In both hypotheses, temperature modulates the metabolic performance and capacity of fish, demonstrating the centrality of metabolism to the whole organism's response to temperature. In the following sections, we will explore how temperature influences metabolic traits and how those effects can provide insight into the response of fish to their environment.

SMR and MMR

Standardized types of metabolic rates are commonly measured to facilitate comparing performance among individuals, species, and methodologies. Standard Metabolic Rate (SMR) represents the baseline metabolic rate of a fish at rest. To measure SMR, fish should be acclimated to the temperature at which they will be tested. Additionally, fish must be fasted to ensure no metabolic activity is associated with meal digestion or assimilation (Specific Dynamic Action), and fish must be undisturbed for long periods to ensure they achieve a quiescent state (e.g., without fin movement) and lull in their diurnal patterns (Chabot et al., 2016).

The TPC of SMR is well defined as a positive exponential relationship (**Fig. 2**A), reflecting, in part, the thermodynamics of cellular processes and chemical reaction rates. As temperature increases the chemical reactions underpinning metabolism increase at an exponential rate. The influence of temperature on SMR is often quantified in terms of a Q_{10} which relates the factorial change in SMR over a change of 10 °C (**Eq. 1**). Q_{10} values for SMR typically range from 2 to 3 depending on whether fish were physiologically acclimated to the test temperature or acutely exposed. A Q_{10} value equal to 1 indicates a rate is temperature independent while a Q_{10} greater than 1 indicates that a metabolic rate is temperature-dependent.

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{T_2 - T_1}} \tag{1}$$

R_1 and R_2 are metabolic rates at temperatures T_1 and T_2 respectively.

Due to the standardized nature of SMR measurements (i.e., acclimated, post-prandial, at rest) alternative measures approximating SMR have developed to account for fish or experimental designs where SMR measurements are infeasible. The most common of these is Resting (or Routine) Metabolic Rate (RMR), which accepts that fish are rarely fully quiescent, and that some species must swim to breathe (e.g., lamnid sharks, tunas) therefore some amount of locomotion is necessary for survival. Additionally, experiments may not acclimate fish to the range of test temperatures, as acclimation can take days to weeks, deciding instead to subject fish to an acute temperature change for testing. Measurements of RMR are commonly used as proxies for SMR, but care should be taken that they likely overestimate the true value of SMR. In the following examples, RMR is commonly used, as fish are not fully acclimated to all test conditions.

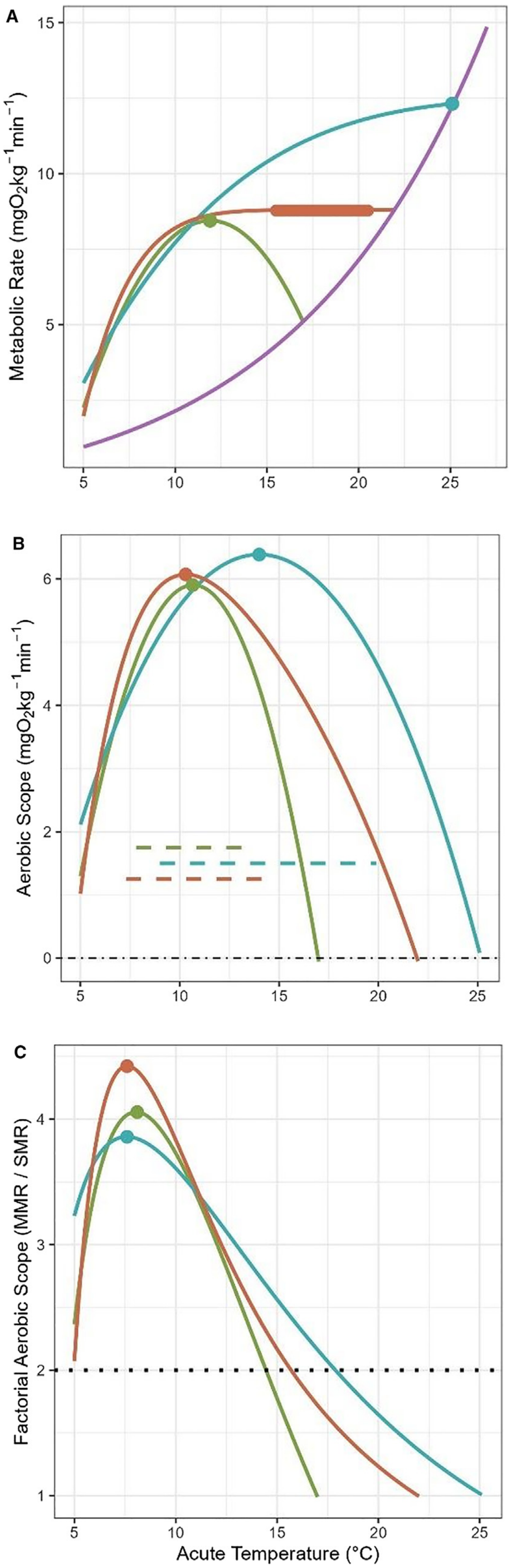


Fig. 2 Hypothetical metabolic traits representing. (A) SMR (purple line) and three different possible MMR curves representing an increasing (Blue), plateauing (Red), or declining (Green) performance at warm temperatures. The resulting (B) absolute aerobic scope (AAS) curves and 90% T_{PEJ} ranges (dashed segments) and (C) Factorial Aerobic Scope (FAS) with a hypothetical FAS threshold of 2 (dotted line) representing an organism with a specific dynamic action equal to double its SMR. Points of optimal performance (T_{OPT}) are indicated by filled circles, note that different traits can exhibit different thermal optima.

MMR

Opposite to SMR is the Maximum Metabolic Rate (MMR), which represents the maximal rate of oxygen consumption that can be sustained by a fish. Typically, fish elicit MMR through exercise, either through manual chasing prior to placement in a respirometry chamber, or in specially designed swimming respirometers (**Fig. 1**B) within which fish must swim against a controlled current, and real-time oxygen consumption can be measured (Norin and Clark, 2016).

Measurement of MMR across a range of acute temperatures yields more diverse relationships than observed with SMR. Generally, MMR is presumed to increase with increasing temperature and then plateau. However, variation in MMR exists among species (**Fig. 2**A), with some exhibiting declines in MMR (Lowe and Davison, 2006; Eliason et al., 2013), an extended plateau (Poletto et al., 2017), or a continuing increase as temperature increases (Zillig et al., 2023b). Furthermore, there is more individual variation in MMR than RMR or SMR which are more consistent among individuals (Norin and Clark, 2016).

For example, the Antarctic fish, *Pagothenia borchgrevinki*, exhibited a clear optimum in MMR near 3 °C and a pronounced decline in MMR at 6 °C. This narrow and steeply peaked MMR performance may reflect physiological adaptation to the cold (ca. −1.8 °C) and stable environmental conditions of the Antarctic's Ross Sea (Lowe and Davison, 2006). Alternatively, in a study of juvenile Chinook salmon, MMRs consistently increased across the range of tested temperatures, including those approaching the upper limits (Zillig et al., 2023a,b). These results challenge the expectations of the OCLTT hypothesis which would expect MMRs to decline as lethal temperatures are approached and the fish's capacity to deliver oxygen declines. Instead, the continual rise in MMR as temperatures reach upper thermal extremes indicates that fish are not suffering a decline in oxygen delivery and therefore the upper critical temperature may instead be structured by temperature-dependent disorganization of the excitable cells as suggested in the TDEE hypothesis.

By studying MMR we gain an understanding of the maximal metabolic rate a fish can produce. Furthermore, quantifying the relationship of MMR across temperatures can provide insight into how fish may be limited or advantaged by future environmental changes. Finally, quantifying the MMR and the SMR of fish enables us to quantify a new metabolic trait, Aerobic Scope, which provides additional insight into the temperature-dependent metabolic performance of a fish.

Aerobic scope

Aerobic Scope (i.e., Absolute Aerobic Scope, AAS) is the difference between a fish's MMR and SMR (AAS = MMR-SMR). It represents aerobic metabolic capacity by capturing the remaining aerobic metabolic potential of a fish once basic physiological needs (i.e., SMR) are energetically provided. Due to the linkage between oxygen delivery and tissue performance, limitations on aerobic scope were theorized to represent limitations on the behavioral and physiological processes of fish.

The relationship between AAS and temperature (i.e., a TPC) has generally been modeled as temperature-dependent bell curves (Eliason et al., 2011; Chen et al., 2015) although instances of temperature-independent, linear TPCs have been observed (Poletto et al., 2017). In instances where AAS TPCs are curvilinear, additional metabolic performance traits can be estimated including the T_{OPT} (temperature of maximum AAS) which is theorized to represent a temperature of optimal physiological and ecological performance (Farrell, 2016). The T_{PEJ} are temperatures at which metabolic capacity is theorized to decline on either side of T_{OPT}, typically defined as an arbitrary percentage (50−90%) of the maximum AAS (Farrell, 2016). Finally, the temperatures at which AAS is equal to zero are defined as $T_{CRIT,}$ and life is not considered viable at these thermal extremes.

The curvature of the AAS TPC relative to temperature is theorized to be indicative of a fish's tolerance for temperature change (**Fig. 2**B). AAS TPCs that are narrow and steeply peaked imply a stenothermal fish, which may inhabit a narrow band of temperatures with a small range of optimal thermal performance (Farrell, 2016). Alternatively, fish that exhibit a broad AAS TPC, with a greater thermal range between pejus temperatures, are thought to be more eurythermal, and capable of tolerating a wide range of environmental temperatures (Farrell, 2016). For instance, common killifish (*Fundulus heteroclitus*) and goldfish, two eurythermal species, exhibit broad aerobic scope curves reflecting their capacity for aerobic metabolism across a range of temperatures (Healy and Schulte, 2012; Ferreira et al., 2014).

Aerobic scope and its corresponding thermal metrics (T_{OPT}, T_{PEJ} and T_{CRIT}) are commonly linked to other aspects of fish physiology. For instance, T_{OPT}, the temperature at which the aerobic scope is maximized, has been found to be associated with an increase in swimming performance (Fu et al., 2022), optimal growth and foraging (Auer et al., 2015), and behavior (Killen et al., 2014). Likewise, T_{PEJ} may have ecological relevance. For example, the thermal window defined by an upper and lower T_{PEJ} may represent the temperature range within which a fish is metabolically capable of completing necessary tasks (e.g., migrating or digesting a meal) (Farrell et al., 2008; Eliason et al., 2013; Farrell, 2016).

An alternative to AAS is the Factorial Aerobic Scope (FAS), which is calculated as FAS = MMR/SMR. As both the constituent traits are temperature-dependent, FAS changes with thermal conditions, although the FAS TPC can have a different shape than a corresponding AAS TPC (**Fig. 2**B vs. C). FAS can be useful for interpreting the relevancy of other metabolic traits. Specific Dynamic Action (SDA) represents the aerobic metabolic costs of digestion and assimilation of a meal. Under the assumption that a fish must be able to digest and assimilate a meal to continue living, the metabolic cost of this action sets an approximate threshold of minimum metabolic performance. In other words, at a given temperature, if a fish cannot muster an AAS greater than its SDA, then that temperature is not suitable for long-term survival. Typically, SDAs have been found to approach 2−3 times an organism's SMR. Therefore, FAS becomes a useful tool in assessing the thermal window under which a fish can effectively assimilate energy

(**Fig. 2**C). Both approaches to quantifying aerobic scope (AAS and FAS) offer distinct insights into the organismal physiology of a fish, sometimes with conflicting results, so care should be taken in matching the selected metric of aerobic scope with the specific research question (Clark et al., 2013; Halsey et al., 2018).

Acclimation and metabolism

The above sections focused on the effects of acute temperature exposure on three primary metabolic rates; SMR or RMR, MMR, and aerobic scope (AAS or FAS). However, prolonged exposure to a thermal condition causes organisms to adjust their physiology in a process called acclimation (or acclimatization if a fish is responding to multiple environmental conditions simultaneously). Acclimation is beneficial to fish by effectively broadening the thermal envelope within which a fish's metabolism can operate optimally. For example, the Trask River population (USA) of juvenile Chinook salmon acclimated to 11 °C exhibits an AAS T_{OPT} of 17.9 °C and a modeled T_{PEJ} range of 11.2−24.5 °C. That same population acclimated to 20 °C exhibits a T_{OPT} of 21.8 °C and a T_{PEJ} range of 14.5−29.2 °C. Therefore, because of acclimation, the overall breadth of performance is estimated to be 11.2−29.2 °C, a 3−4 °C increase over either the 11 or 20 °C acclimated physiology alone (Zillig et al., 2023a). This change in temperature-dependent performance is a consequence of multiple physiological changes occurring at sub-organism scales.

Thermal acclimation in metabolic capacity is the integrative outcome of phenotypic plasticity among multiple physiological traits. Organisms may upregulate or downregulate the expression of specific genes and synthesize different protein isoforms, which may operate more efficiently under the new temperature regime. For example, lake whitefish (*Coregonus clupeaformis*), a cold-water species, acclimated to 18 °C exhibited greater transcription of heat shock proteins (*Hsp70* and *Hsp47*) compared to fish acclimated to 6 °C (Manzon et al., 2022). Because heat shock proteins are essential for maintaining protein function when an organism is faced with stress such as elevated temperatures, warm acclimation may prepare the cold-water Lake Whitefish physiologically to prevent cellular damage at elevated temperatures.

Another cellular response to thermal acclimation is the alteration of cellular phospholipid membrane composition. The fluidity and flexibility of cellular membranes are essential to proper cell function and can be altered by changing the composition of different lipid types. Cellular membranes become more rigid as temperature decreases, altering their permeability and affecting cellular processes. Greater fluidity is achieved by increasing the proportion of unsaturated fatty-acid lipids in the cellular membrane. This phenomenon has been observed in rainbow trout (Hazel, 1979), western mosquitofish (*Gambusia affinis*), guppies (*Lebistes reticulatus*; Knipprath and Mead, 1966), and carp (*Cyprinus carpio*; Farkas and Csengeri, 1976) acclimated to cold temperatures. These species counteracted the cold-induced reduction in membrane fluidity by increasing the proportion of unsaturated fatty acids.

As noted above, increasing the thermodynamics of cellular processes (i.e., warmer temperatures) increases the baseline metabolic rate of organisms. For example, a fish acclimated to cold water conditions and acutely trialed at warm test temperatures will have an elevated RMR; however, as the fish acclimates to a warm temperature condition, it may physiologically compensate for the warming, resulting in a lower RMR at the given test temperature (**Fig. 3**). A study of juvenile Chinook Salmon acclimated at 11, 16, and 20 °C showed that warm acclimation to 16 or 20 °C decreased RMR across the range of test temperatures (8−25 °C). Specifically, the RMR of fish acclimated to 20 °C was 69−80% less than that of fish acclimated to 11 °C (Zillig et al., 2023a). Reduction of RMR with increasing acclimation temperature aids the fish in reducing metabolic costs associated with warm temperatures.

In the same study, the MMR of juvenile Chinook salmon was likewise reduced when acclimated to warm temperatures (**Fig. 3**). Fish acclimated to 11 °C were capable of eliciting higher MMRs across the thermal gradient than fish acclimated to 20 °C (Zillig et al., 2023a). Salmon are generally considered to be a cold-water species, capable of tolerating temperatures approaching 0 °C, and therefore the decline in MMR associated with warm acclimation (20 °C) indicates the physiological challenge of warm acclimation.

The impact of thermal acclimation on AAS and FAS depends upon the acclimation effects of SMR and MMR. In the study on juvenile Chinook salmon, warm acclimation decreased both the SMR and to a greater extent the MMR across a range of temperatures. This resulted in an overall decrease in AAS of warm-acclimated fish, relative to their cold-acclimated counterparts, reflecting their typically cooler natural habitats (Zillig et al., 2023a). However, warm-acclimation "shifted" AAS so that a juvenile salmon's T_{OPT} and T_{PEJ} were all determined to be warmer than a cold-acclimated fish (**Fig. 3**), which would theoretically improve organism fitness under a warmer thermal regime.

Additional stressors

The thermal acclimatization response of metabolic rates can be further impacted by additional stressors such as oxygen limitation, acidification, and pollutants. Oxygen is of primary concern, both due to its central role in metabolism, and the inverse relationship between temperature and oxygen solubility in water; as water temperatures increase less oxygen can be dissolved in water. Therefore, it is common for wild systems to become hypoxic (low oxygen) as temperatures warm. Given the reliance of aerobic metabolic activity on oxygen availability, hypoxic conditions alter the relationship between metabolic capacity and temperature (Claireaux and Chabot, 2016). Typically, when fish are exposed to low-oxygen conditions their aerobic scope contracts, reflecting the increased difficulty of acquiring oxygen from the water to meet the demand of the organism's tissues. Additionally, fish may increase their anaerobic metabolic activity to ensure energy is supplied to their tissues despite the lack of oxygen. The concentration (or partial

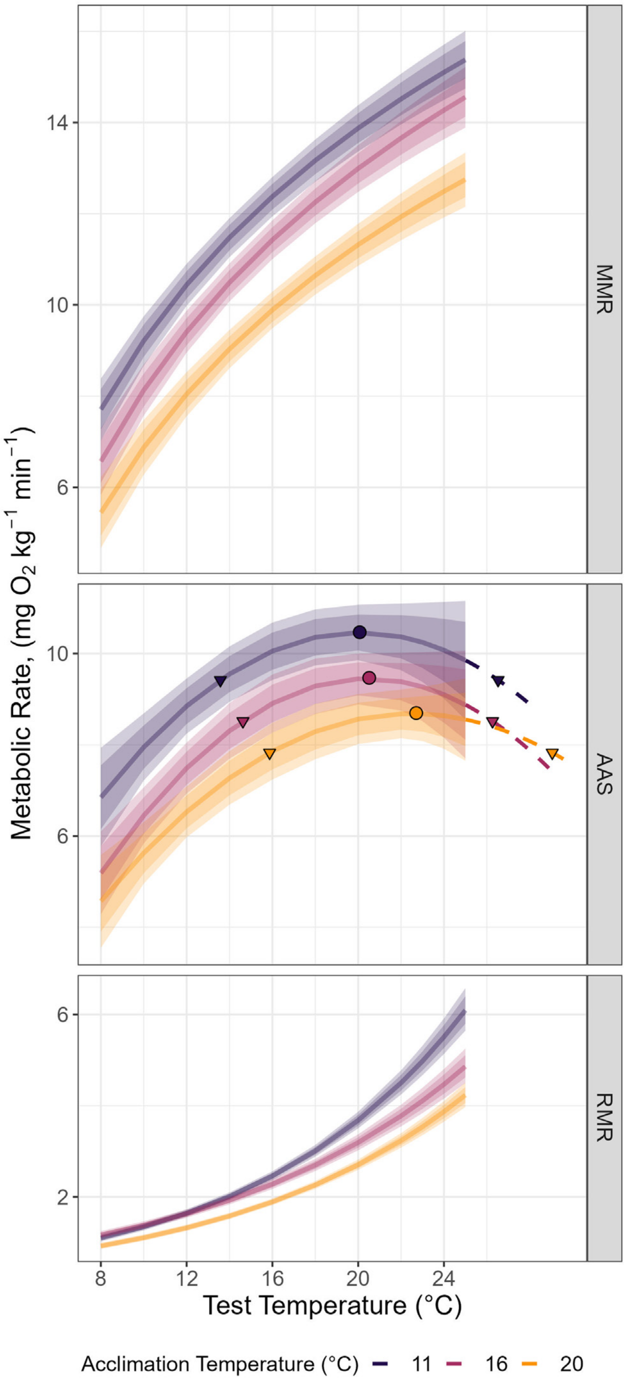


Fig. 3 MMR, AAS, and RMR for a single population of juvenile Chinook Salmon (Priest Rapids population) acclimated to three temperatures. Acclimation to warmer temperatures reduced metabolic rates over the tested range. The shaded region represents the 50% (dark) and 89% (light) credible interval of the modeled metabolic rate relationships while the dotted line are extrapolation of the AAS TPC to the acute thermal maxima of each group. The circle represents the T_{OPT} while the inverted triangles represent the T_{PEJ}. Data from Zillig et al. (2023a): https://doi.org/10.25338/B8P63W.

pressure) of oxygen in the water under which an organism cannot maintain its SMR is termed P_{CRIT}. Measurements of P_{CRIT} and metabolic rates under hypoxic conditions can provide insight into the hypoxia tolerance and anaerobic capacity of fishes.

A respirometry study on Atlantic cod (*Gadus morhua*) acclimated to three temperatures (2, 5, and 10 °C) and then challenged with hypoxia provides an informative case study. Researchers found that hypoxic conditions reduced RMR and MMR, and consequently AAS across all thermal acclimation groups. At full oxygen saturation, the warm-acclimated groups exhibited higher RMR, MMR, and AAS than the cold-acclimated groups (Fig. 4). This pattern was consistent even under hypoxic conditions with all thermal

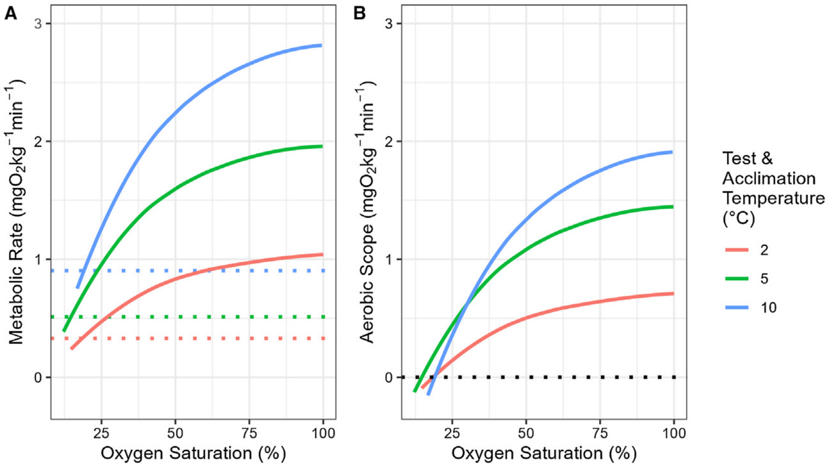


Fig. 4 The effect of hypoxia (Oxygen Saturation) on the metabolic performance of Atlantic Cod (*Gadus morhua*). (A) The MMR (solid lines) and SMR (dotted lines) of cod acclimated to 2, 5, or 10 °C and tested at their acclimation temperatures. (B) The AAS (solid lines) is calculated as the difference between the MMR and AS across oxygen saturation. The dotted black line indicates an AAS $= 0$, and the intersection of the AAS line with this dotted line is a P_{CRIT}. Data modified from Claireaux et al. (2000).

acclimation groups exhibiting an approximate 20% reduction in MMR at 50% oxygen saturation and a P_{CRIT} at ca. 20% oxygen saturation (Claireaux et al., 2000). Understanding the mixed effects of temperature and oxygen on fish metabolism can provide important insight into how fish cope with environmental changes which commonly include both changes in temperature and oxygen availability.

Further evidence of the constraining effect of hypoxia on metabolic capacity can be found in studies where fish are tasked with swimming under hypoxic conditions. Research on striped bass (*Morone saxatilis*) found that individual fish always exhibited greater hypoxia tolerance (defined as the time until loss of equilibrium) when at rest as opposed to swimming against a current (Nelson and Lipkey, 2015). Similar work on mulloway (*Argyrosomus japonicus*) found that as hypoxic conditions became more severe (75% vs. 50% vs. 25% oxygen saturation) the SMR, MMR, and AAS all declined accordingly (Fitzgibbon et al., 2007). The U_{CRIT} (the maximum sustained swimming speed) likewise declined with increasing hypoxia. However, mulloway were able to preserve optimal swimming capacity at 75% oxygen saturation, with declines at 50 and 25% oxygen saturation. This result hints at the physiological capability to allocate aerobic capacity to swimming as needed under conditions of light hypoxia. Future work is necessary to determine how temperature exposure may influence mulloway's ability to moderate hypoxic conditions.

Adaptations

Responses of metabolic performance to both acute and more chronic thermal conditions demonstrate that different fish species have adapted to their thermal environment. These metabolic responses can provide insight into how fish may adapt to novel thermal conditions (i.e., adaptive capacity), and multiple hypotheses have arisen attempting to describe the mechanisms underlying temperature's influence on metabolism, including the Universal Temperature Dependence hypothesis (UTD) and the Evolutionary Trade-Off hypothesis (ETO).

The UTD (Gillooly et al., 2001) posits that an organism's metabolic rate is a simple function of its body mass, temperature, and the activation energy of a rate-limiting biochemical reaction. Therefore, the UTD states that the thermal kinematics of a highly-conserved rate-limiting reaction determines the effects of temperature on overall organism metabolism. A prediction of this hypothesis is that the effect of temperature on metabolism, primarily SMR, should be the same both inter- and intraspecifically. In other words, the change in SMR with temperature (i.e., Q_{10}) from different species across a thermal gradient (polar to tropical) should match the Q_{10} of conspecific individuals acclimated across a range of temperatures. However, residual variations in metabolic rate among organisms are difficult to explain and are attributed to species-specific differences in ecology (Gillooly et al., 2001; Clarke, 2004). As evidence against the UTD, the Q_{10} for interspecific comparisons among teleosts was found to be 1.83 while the mean of several intraspecific Q_{10} values was 2.36, indicating species-specific metabolic responses to temperature (Clarke, 2004).

The ETO accepts the first principle assumptions of the UTD as applied to simple systems, but posits that organisms are complex and that natural selection could act upon this complexity, yielding variation both intra- and interspecifically (Clarke, 2003). Therefore, the effect of temperature on an organism's metabolic rate reflects evolutionary pressures on myriad physiological traits (organ size, tissue efficiency, biochemical pathways and proteins, etc.) that optimize overall metabolic performance to fit particular environments and life histories (Clarke, 2004). As an example, the Metabolic Cold Adaptation Hypothesis (MCA), which could be considered a specific case of the ETO, posits that the metabolic rate of cold-adapted species (e.g., polar fishes) is higher at low temperatures than would be predicted from the extrapolation of metabolism of a temperate or tropical species to those same cold temperatures (Holeton, 1974; Clarke and Johnston, 1999). This theorized elevated metabolic rate would be a result of adaptation to frigid environments. Acceptance of the MCA is contentious with several studies on teleosts providing opposing conclusions (Holeton, 1974; Clarke and Johnston, 1999; Steffensen, 2002; White et al., 2012; Watanabe and Payne, 2023).

A recent meta-analysis indicated that the MCA and UTD may both be supported, albeit for different taxonomic groups (Watanabe and Payne, 2023). Interspecific comparisons of elasmobranchs (sharks and rays) found higher Q_{10} values than estimates of teleost Q_{10} values, indicating that elasmobranch physiology may adhere to predictions of the UTD hypothesis while teleosts may follow predictions of the MCA hypothesis. Theorized explanations for the taxon-specific temperature relationships revolve around differences in metabolic pathways and osmoregulation (Speers-Roesch and Treberg, 2010; Watanabe and Payne, 2023). These differences are consistent with the ETO, which predicts that temperature-dependent metabolic performance reflects the energetically driven adaptations of species. Differences in the adaptive capacity of different taxonomic groups are important when considering the impacts of rapid environmental changes. Continued research studying the interaction between temperature and fish metabolism will refine these hypotheses.

Differences in fish metabolic performance can also reveal adaptation to different thermal regimes within a single species. Isolated populations exposed to unique thermal conditions (e.g., cold and stable, or hot and variable) may undergo natural selection for metabolic optimization to those conditions. Salmonid species have been repeatedly studied to investigate the drivers of thermal adaptation via measurements of metabolic capacity (Eliason et al., 2011; Chen et al., 2015; Verhille et al., 2016; Poletto et al., 2017; Zillig et al., 2023a,b). Salmonids make for excellent study species for this research due to the number of testable populations and the natural behavior of natal homing which genetically isolates populations (**Fig. 5**). Work on six populations of adult sockeye salmon found that the AAS TPC curve exhibited T_{OPT} consistent with the historic temperature ranges of each population's natal river (Eliason et al., 2011). Winter-run Chinook salmon, an endemic population from California, historically spawned and reared in atypically cold, spring-fed systems. Research on this population indicated that they have reduced aerobic performance when acclimated to warm temperatures, specifically their T_{OPT} declines when acclimated to 20 °C vs. 11 °C (Zillig et al., 2023b). A comparison of six populations of fall-run Chinook salmon found that populations that experienced warmer temperatures during the juvenile rearing period exhibited greater metabolic capacity when acutely tested at high temperatures ($>$20 °C; (Zillig et al., 2023a)). Interestingly, warm acclimation mitigated differences among populations, exposing an interaction between acclimation and adaptation. Finally, work on *O. mykiss*, another cosmopolitan and well-studied species, has identified populations in Central California (Verhille et al., 2016), Western Australia (Chen et al., 2015), and desert plateaus in Oregon, USA (Rodnick et al., 2004) that exhibit high-temperature metabolic capacity consistent with local adaptation to thermal extremes. These results are supported by genetic research, that investigated single-nucleotide polymorphisms (SNPs) among populations of steelhead (anadromous *O. mykiss*; (Micheletti et al., 2018)) and redband trout (*O. mykiss gairdneri*; (Chen et al., 2018)). Both studies found that SNPs from genomic regions associated with cardiac traits are undergoing selection. These selective pressures are associated with environmental characteristics including temperature and hint at a genotypic underpinning for the relationship between environmental temperature and metabolic capacity.

Regional endotherms

Metabolic activity, even in ectotherms, generates heat. In endothermic animals (e.g., mammals, birds) this metabolic heat is preserved to allow the organisms to maintain thermal homeostasis at optimal physiological temperatures across a breadth of environmental conditions. In an aquatic environment, heat is rapidly lost and therefore endothermy is too metabolically costly for the vast majority of fishes (Brill et al., 1994; Bernal et al., 2001). However, an interesting case of thermal physiology and metabolism are regional endotherms (e.g., lamnid sharks, tunas, and billfish), which maintain elevated body temperatures in specialized regions of their bodies. Regional endothermy is hypothesized to improve the predatory effectiveness of tuna, billfish, and lamnid sharks which routinely cross thermoclines and are therefore exposed to a wide and dynamic range of temperatures (Bernal et al., 2001). For example, billfish (e.g., marlin and swordfish) are able to maintain higher-than-ambient temperatures in their eyes, using a modified eye muscle tissue that generates heat. Warming their eyes and brain above the temperature of the environment is hypothesized to increase visual acuity and neural processing leading to more successful hunting (Block, 1986; Dickson and Graham, 2004).

An extreme example of homeothermy is the pelagic and circumglobally distributed opah (*Lampris gutattus*), which exhibits endothermy throughout most of its body's tissues using heat generated by its pectoral musculature both through both swimming action (Wegner et al., 2015) and non-shivering thermogenesis (Franck et al., 2019). This heat is then retained through countercurrent heat exchangers located at the gills (Wegner et al., 2015). This whole-body endothermy, and consequently above-ambient cardiac and cranial temperatures allows the opah to hunt in deeper, colder waters than other regional homeotherms (e.g., tunas and billfishes).

Relevance to conservation and ecology

Technological advances in the field of respirometry have made the acquisition of metabolic data considerably easier and faster. Subsequently, the cost of acquiring such data has decreased and the application of these tools has diversified. Thermal metabolic physiology is now being incorporated into studies of fish ecology, behavior, and aquatic and marine conservation. Within these fields, the tools of metabolism have been applied to investigate the response of species to climatic change (Duncan et al.,

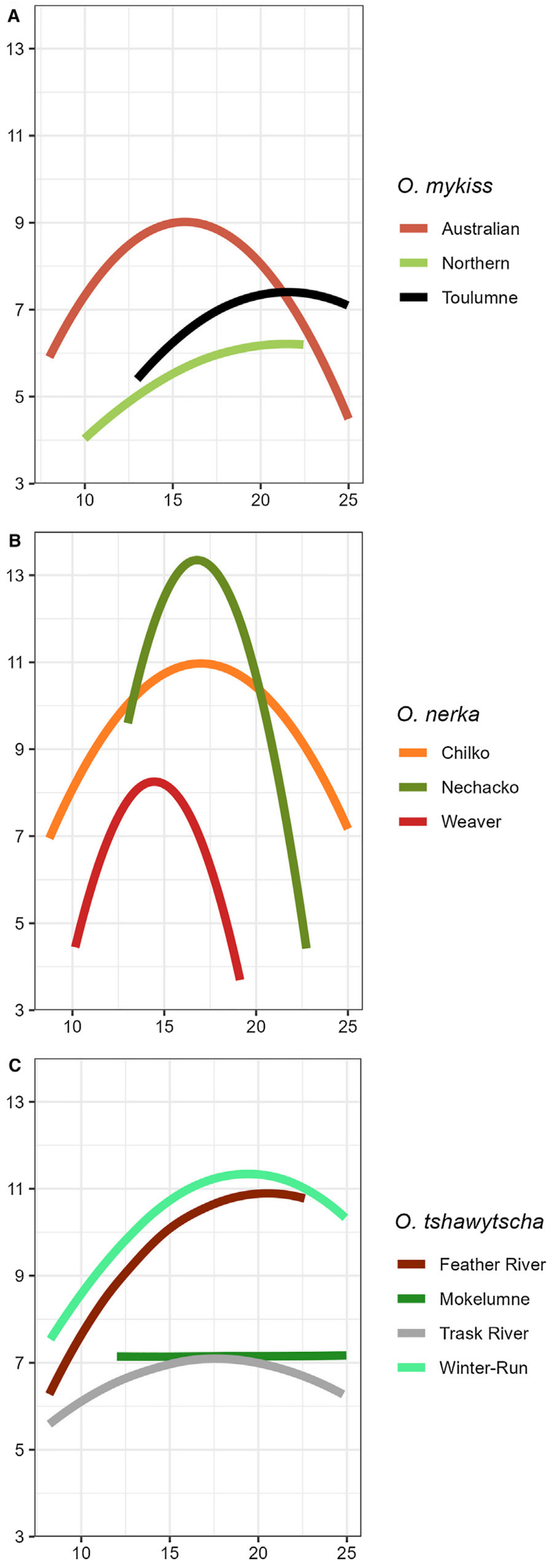


Fig. 5 An assemblage of metabolic rates from three salmonid species. (A) Rainbow Trout (*O. mykiss*). (B) Sockeye Salmon (*O. nerka*) (C) Chinook salmon (*O. tshawytscha*). (A) Data from (Fry, 1948; Chen et al., 2015; Verhille et al., 2016). (B) Data from Eliason et al., (2011), (C) Data from Zillig et al. 2023a,b. Data were extracted from plots in Eliason et al., 2011; Verhille et al., 2016; Zillig et al. 2023a,b.

2020), and to develop theories of how temperature-dependent metabolism structure fish behavior and interspecific interactions (Brownscombe et al., 2022; McInturf et al., 2022).

The abundance of metabolic data has allowed the field to begin integrating metabolism and metabolic TPCs with aspects of fish behavior, distribution, and ecology. A novel energetics-performance framework posits that the ecological context of fish (e.g., competition for food, risk of predation or disease, etc.) determines how fish behavior and fitness are supported through energy expenditure and metabolic performance (Brownscombe et al., 2022). Under this framework, metabolic traits such as T_{OPT} are contextualized ecologically with an understanding that the presence of competitors, predators, or disease vectors may alter the interpretation of metabolically optimal thermal conditions. A complementary framework considers that fish possess both a fundamental and ecological thermal physiology (Zillig et al., 2021). The fundamental thermal physiology represents, the temperature-dependent metabolic capacity of a fish based on its intrinsic phenotypic traits (e.g., heart volume, gill surface area, citrate synthase isoforms). The ecological thermal physiology is then produced through the interaction of a given fish's fundamental thermal physiologies and the fundamental thermal physiology of its biotic interactors, such as predators or competitors. Both approaches acknowledge that metabolic TPCs and their derivative measures of T_{OPT}, $T_{PEJ,}$ and T_{CRIT} may not reflect the optimum ecological conditions of fish contending with the complex energetic costs of wild ecosystems and that integrating the temperature-dependent metabolic performance across interacting species may be necessary.

As an example of this integration of metabolic performances, recent work investigated the role of temperature on trophic interactions. The temperature-dependent metabolic performance and burst bass (*Micropterus salmoides*), a predator species, and their prey, juvenile Chinook salmon. Trophic interactions were shown to not be strongly associated with aerobic metabolic performance, but did reflect the burst swimming capacity, which is supported, in part, by anaerobic metabolism (McInturf et al., 2022). The use of metabolic data in understanding ecological dynamics is a developing application and much work is still needed to refine the practices of integrating metabolic performance across species.

Finally, metabolic and hypoxia tolerance traits have been combined to scale organismal physiology to the ecosystem and across landscapes. Tools such as metabolic index (ϕ) which is the ratio of O_2 supply to the demand of a fish at rest (SMR), have been used to translate between species distributions and their oxythermal physiology (Deutsch et al., 2020). For example, work on *Chrysoblephus laticeps*, a South African reef fish, used SMR and MMR measurements in combination with empirically derived hypoxia tolerance data to define the metabolic index values associated with presence of *C. laticeps* throughout its range (Duncan et al., 2020). This allowed the authors to identify a species-specific metabolic index threshold ($\phi \geq 2.78$), above which *C. laticeps* may be found. Notably, the range of *C. laticeps* appeared limited by different abiotic conditions (oxygen vs. temperature) in different regions of its range. Metabolic index values predicted for *C. laticeps* across its range, using models of oxygen and water temperature, can be used to identify where *C. laticeps* may be resilient or at risk to future environmental change.

Conclusion

In summary, the capacity of organisms, and therefore populations to persist relies upon their ability to metabolize. Metabolizing energy typically relies upon the consumption of oxygen to fuel the chemical digestion of energy resources and results in the production of ATP. The protein-facilitated reactions within this process are governed by the temperatures at which they occur and the availability of reactants (e.g., oxygen, glucose). This inherent temperature-dependency is integrated into temperature-dependent organismal responses (e.g., growth rates, locomotion velocities) which can be approximated via measurement of the metabolic rates. Two primary metabolic rates, SMR and MMR, form the basis of additional metrics such as AAS and FAS, and specific temperature landmarks such as T_{OPT} and T_{CRIT}. This standardized approach to interpreting metabolic TPCs allows cross-study comparison of metabolic rates from species around the globe. Such broad comparisons have enabled researchers to document the response of fish to both acute and chronic thermal exposure. These studies have revealed the impressive physiological dynamics that allow fish to metabolically compensate for changes in their environment and suggest that natural selection may act on the metabolic capacity of individual fish yielding adaptive differences among populations and species. Through the study of metabolic performance both within and across species, we have gained insights into the evolutionary processes that tailor species to their environment. Finally, our understanding of the relationship between fish metabolism and ecological performance is constantly developing. Researchers are developing metabolic tools and integrating metabolism into predicting species' response to environmental change. Using metabolism as a tool to understand the impact of temperature on fishes around the world will provide necessary information to combat conservation challenges in both marine and freshwater ecosystems.

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See Also: Behavioral responses to temperature in fishes; Cardiac thermal acclimation and adaption of the heart to extreme temperatures; Case study: The desert pupfish; Effects of climate warming; Effects of temperature: An introduction; Integrated responses of the heart to acute changes in temperature; Measures of thermal tolerance; Responses and adaptations of cellular metabolism to temperature; Thermal sensitivity of cardiac performance: Implications for sustainable salmon fisheries.

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