Chapter 11

45 years of “The respiratory and circulatory systems during exercise” in *Fish Physiology*, as per David R. Jones and David J. Randall

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Chapter Outline

Rummer discusses the impact of Jones and Randall’s chapter “The respiratory and circulatory systems during exercise” in *Fish Physiology*, Volume VII published in 1978.

This classic contribution established a foundational framework in the field of fish physiology and the series of books of the same name and, as a result, has been pivotal in shaping research trajectories for decades. In this chapter, Jones and Randall define exercise as the quintessential, unifying stressor that is encountered by all animals and a principle that has become a focal point for extensive research across diverse taxa, habitats, populations, and environmental conditions. From a personal perspective, Jones and Randall’s cornerstone work in exercise physiology in fishes has been instrumental in guiding my own research into the remarkable parallels between the athletic prowess of fish and human athletes. Indeed, it has catalyzed a career-long pursuit to understand

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the endurance, performance, and adaptations of these aquatic athletes, uncovering similarities that resonate beyond their aquatic environments and reflecting broader principles of resilience and vulnerability. This approach has not only shaped my research focus but has also helped me enhance my public engagement and deepen my understanding of the intricate dynamics at play within aquatic ecosystems.

1 What is exercise in fish?

Jones and Randall describe exercise as work performed by the locomotory muscles and emphasize that exercise leads to an increase in the rate of energy conversion above resting rates. It can range from sustained swimming against a current for long periods of time (i.e., sustained, endurance; also see Webb, 1998) to burst-type activities associated with predator avoidance or prey capture (also see Domenici and Blake, 1997). This heightened activity associated with exercise necessitates a surge in energy conversion rates to fuel not just the muscles responsible for movement but also the cardiac and respiratory systems. Fish increase the rate of gas exchange at the gills and tissues during exercise to meet the heightened oxygen demand. The heart and respiratory muscles work in tandem to augment oxygen uptake to fulfill the increased demand brought on by exercise.

In this seminal contribution, Jones and Randall focus intently on the physiological adaptations that enable fish to boost gas exchange rates at the gills and tissues, ensuring an adequate supply of oxygen to support the energetic costs of exercise. This exploration is crucial as it sheds light on the intricate balance of the respiratory and circulatory systems in meeting the metabolic demands of fish during periods of increased activity, providing insights into their overall fitness and survival. In response to the demands of exercise, fish exhibit a remarkable adaptation by significantly increasing their ventilation volume. This physiological adjustment is imperative for enhancing oxygen uptake from the water. During periods of increased activity, such as sustained swimming or escape responses, the oxygen demand of the fish's muscles escalates. To meet this heightened demand, fish increase the flow of water over their gills, thereby augmenting the volume of water ventilated. This increase in ventilation volume is not just about moving more water; rather, it is intricately tied to the efficiency of oxygen utilization. By passing more water over the gills, fish maximize the extraction of available oxygen, ensuring a steady supply to their tissues. This adaptation is particularly vital in environments where oxygen levels may be variable or limited. The increased ventilation volume, therefore, plays a dual role: it meets the immediate oxygen needs of the fish during exercise and enhances the overall efficiency of oxygen utilization, which is a critical factor in the fish's ability to sustain prolonged periods of physical activity. This adaptation underscores the fish's remarkable ability to modulate its respiratory system in response to varying metabolic demands, reflecting an intricate balance between energy expenditure and efficient oxygen uptake. Complementing this foundational perspective, Claireaux et al. (2005) link swimming performance directly to cardiac pumping ability and cardiac anatomy in rainbow trout. Their research offers empirical evidence on how the cardiovascular system adapts to support the energetic costs of exercise, thereby deepening our understanding of the physiological mechanisms that underlie fitness and survival. This integration of cardiovascular function with swimming performance exemplifies the complex interplay of physiological systems in response to exercise in fish.

2 How is exercise performance measured and assessed in fish?

Jones and Randall refer to various methodologies used to quantify the physical exertion of fish. They also note and cite another fellow English-turned-Canadian fish physiologist, F. E. J. Fry, also with some of the most classic work in the field, still today, to clarify standard, routine, and active metabolism as terms to refer to basal metabolism, metabolism associated to a degree of random activity, and the maximum sustained metabolic rate, respectively (Fry, 1971). This would later become a topic heavily investigated among fish physiologists in terms of experimentally measuring and estimating such limits and comparing between species, conditions, etc. (e.g., see Chabot et al., 2016; Killen et al., 2017; Norin and Clark, 2016; Rees et al., 2024; Rummer et al., 2016).

Indeed, Jones and Randall discuss the use of “water tunnels,” now commonly referred to as swim tunnels, which allow for the control and measurement of swimming speed as a means to simulate natural exercise conditions. Essentially, fish are placed in a controlled flow of water, and their swimming endurance and speed are measured. This can be adjusted to simulate different environmental conditions. Cardiorespiratory responses are monitored by measuring oxygen uptake or consumption rates, blood lactate concentrations, and changes in heart rate, to name a few. These physiological indicators provide insights into the metabolic rate and the capacity for oxygen delivery to the muscles during activity. In line with this, Yousaf et al. (2023) recently reviewed the use of heart rate bio-loggers via their team’s studies assessing stress during critical swimming speed tests on farmed Atlantic salmon to further emphasize the importance of such methodologies in understanding the physiological impacts of exercise on fish.

An array of data can be collected from swimming protocols. For example, depending on system design, oxygen uptake rates (MO_2) can be obtained at any swimming speed (U), and the relationship between MO_2 and U can be established. This relationship can depend on life stage (e.g., across ontogeny in sockeye salmon, *Oncorhynchus nerka*; Brett, 1964) and differ by species (e.g., comparisons to rainbow trout, *Oncorhynchus mykiss*; Rao, 1968). Cost of swimming can also be determined, and this information can be combined with knowledge of energy substrates used to define total energy expenditure during swimming. That said, U can be expressed in a variety of ways. The speed at which fish are able to swim in the flume is often related to their critical swimming speed (U_{crit}), which is the maximum speed they can maintain before fatigue. U_{crit} is a commonly used measure of sustained swimming performance and defined as the highest speed a fish can maintain for a prolonged period without fatigue, usually measured over a series of increasing velocities in a swim tunnel until the fish can no longer keep pace with the water flow. U_{crit} is used to assess the aerobic swimming capacity of fish and is an indicator of their overall cardiovascular and muscular fitness. It can be influenced by various factors, including water temperature, fish size, species, and the state of acclimation to different flow regimes. In contrast, burst swimming speed (U_{burst}) is the maximum speed a fish can achieve in short, intense bursts, typically used during escape responses or predator-prey interactions. Unlike U_{crit}, U_{burst} is anaerobic and can only be sustained for a few seconds to a couple of minutes, depending on the species and conditions. U_{burst} is measured by observing the fish during these high-intensity efforts, either in a swim tunnel with a sudden increase in flow or in an open area where the fish can swim freely without constraint. Both swimming measurements provide valuable information about different aspects of fish swimming performance. While U_{crit} is more relevant to migratory behavior, endurance swimming, and the ability to cope with steady currents, which is important for understanding how fish may navigate their environment, particularly in the context of riverine habitats or steady ocean currents, U_{burst} is crucial for understanding escape responses, predator evasion, and the capture of prey, which are critical for survival in the wild. This would also become a topic (Domeneci and Blake, 1997) heavily investigated at the University of British Columbia (UBC), where Jones and Randall were based, by then PhD student, Paolo Domenici, and his supervisor, Bob Blake, who was a dear colleague of Jones and Randall.

3 Other metrics derived from exercise studies

Regardless of U_{crit} or U_{burst} protocols, so many other metrics can be derived from these studies, which would catalyze several subsequent decades of research. Moreover, Jones and Randall stress that no matter how closely we aim to simulate stream, river, and ocean conditions and force fish to swim to maximal performance, none of these conditions are exactly what fish experience in their natural habitat, and therefore it is crucial to understand the relationship between these various measures and other parameters. For example, tail beat frequency and amplitude can also be calculated these studies and provide information on the swimming kinematics, efficiency, and the type of swimming mode used (e.g., steady vs. burst swimming). With these swimming protocols, electromyography (EMG) can be added to record muscle activity patterns during swimming to understand muscle function and fatigue. Indeed, studies have focused on power output at various U to find the highest speeds at which the cost of transport is lowest. Given the relationship between oxygen uptake and speed, the efficiency of swimming increases to a point and then decreases with speed (Webb, 1971), which is important information that translates to various ecological and applied scenarios for fish. Heart rate can be monitored to assess the cardiovascular response to different swimming speeds and exercise intensities, and the rate and depth of opercular movements, which indicate the ventilation effort required to maintain aerobic metabolism during swimming, can also be measured. Metabolites may be most telling, as Jones and Randall suggest. Blood lactate concentration can be measured in cannulated fish during exercise or post-exercise to assess the level of anaerobic metabolism during high-intensity swimming. Likewise, other blood parameters, including pH, hematocrit, and concentrations of metabolic substrates and hormones, can be measured to assess physiological stress and energy utilization. By varying the water temperature in the swim flume, researchers can assess the thermal tolerance and the effect of temperature on swimming performance, which comes with its own challenges (e.g., failure temperatures, and what cardiorespiratory mechanisms are at play, see Eliason et al., 2013 and others). Finally, the time it takes for a fish to become exhausted at a given swimming speed, which can be an indicator of endurance and overall fitness, as well as post-exercise recovery rates for all the physiological parameters mentioned can provide insights into the fish's ability to recover from exertion. This approach has certainly catalyzed a comprehensive understanding of the multifaceted nature of exercise in fish, encompassing the physiological, biomechanical, and ecological dimensions of their swimming capabilities.

4 Use of water tunnels to exercise fish over the years

The first water tunnels for fish, also known as swim flumes or swimming respirometers, were developed in the 1960s. A pioneer in this field was Brett (1964), from the Fisheries Research Board of Canada in Nanaimo, British Columbia, not too far from the UBC where Jones and Randall were based. Brett's seminal work on the metabolic rates and swimming performance of salmonids in these swim tunnels laid the foundation for much of the current research on fish exercise physiology. I still remember using one of these large Brett-type swim flumes in the basement of the Department of Zoology at UBC during my PhD. While the Brett swim tunnel is typically an open-flow system, which can more closely replicate natural conditions for swimming fish, the Blazka swim tunnel—also designed in the 1960s (Blazka et al., 1960)—is a closed respirometry system, ideal for measuring oxygen uptake rates and other metabolic parameters during exercise. The Blazka swim tunnel recirculates water in a loop, creating a uniform flow and reducing the amount of water needed. However, this design may require more frequent water quality management to ensure fish health. Initially designed for smaller fish species, the Blazka tunnel allowed precise control of water flow and oxygen uptake measurements. In contrast, Brett's tunnels could be scaled up for larger fish and studies requiring longer swimming distances, though they required more space and could be more costly. The open system is easier to maintain for water quality over longer periods, beneficial for certain behavioral studies. Both types of swim tunnels have been essential in advancing fish exercise physiology, despite logistical constraints of the times. To address these challenges, Bell and Terhune (1970) provided a comprehensive guide on water tunnel design, offering detailed insights into construction and optimization for studying fish swimming behavior and physiology. This guidance overcame early logistical challenges, paving the way for evolving swim flumes that accommodate a wide range of species and experimental conditions, enhancing our understanding of fish locomotion and its ecological implications.

Since these early days, swim flumes have progressed tremendously, accommodating the tiniest vertebrates (e.g., larval coral reef fishes; Downie et al., 2023) to 100 kg sharks in a "mega-flume" (Payne et al., 2015). Technological advancements have also improved these tools, now allowing a wider range of species to be investigated under diverse conditions. High-resolution sensors and computer models enable detailed analyses of fish swimming in complex flow conditions. Additionally, 3D printing allows researchers to create custom-designed structures and components for swim tunnels and respirometry chambers, essential for small-scale species (Huang et al., 2020). Customization helps create controlled environments to study fish swimming behavior and physiology. While swim flumes offer numerous benefits in measuring physiological, morphological, and behavioral aspects of exercise, they are time-consuming and often allow only one fish to be swum at a time. Contemporary studies have compared swimming respirometry with various chase protocols as proxies for labor-intensive methods. Swim flumes simulate natural conditions, providing insights into the ecological relevance of fish swimming performance and highlighting the importance of replicating natural flow conditions to understand adaptive swimming behaviors in different species. Studies using swim flumes to explore physiological responses to environmental stressors during exercise have been pivotal in understanding the impacts of climate change on marine life (Rummer et al., 2016). These studies show swim flumes are crucial for understanding broader ecological and environmental contexts. Additionally, research has investigated energy expenditure and metabolic rates during sustained swimming, providing a comprehensive view of fish physiology and its implications for survival and fitness in the wild (Roche et al., 2013). The evolution of swim flumes from rudimentary setups to sophisticated systems equipped with advanced technology has revolutionized the study of fish physiology and behavior, enabling deeper insights into fish locomotion complexities and its ecological implications.

While the development of swim flumes has been instrumental in studying fish exercise, it is the intricate physiological responses, particularly cardiovascular and respiratory adaptations, that truly illuminate the complexities of exercise in fish. Exploring fish exercise performance via swim flumes, especially sustained swimming (Webb, 1998), and other strategies has led to a re-evaluation of how exercise is measured and interpreted. Such approaches have highlighted the importance of both aerobic and anaerobic metabolic pathways in determining exercise capacity (Rees et al., 2024) and deepened our understanding of physiological limits and fatigue mechanisms in fish (Farrell, 1997).

5 Exercise and the respiratory system

Jones and Randall discuss how the capacity for oxygen uptake in fish is influenced by various factors. The focus is on how changes in these components—including the surface area of the gas exchanger, its permeability, the distance between water and blood, and the difference in oxygen partial pressure across the exchange surface—affect oxygen uptake during exercise. The maximum oxygen uptake in fish is primarily constrained by morphometric factors, like gill surface area and diffusion distance, rather than physiological ones. There is a general relationship between these morphometric factors and metabolism, often explored in relation to body weight or mass. Metabolism follows a power function in relation to body mass. For example, in tench (*Tinca tinca*), as body weight increases, the capacity of the gas exchanger becomes a limiting factor for both resting and active metabolic needs. In contrast, for salmonids, the relationship between gill surface area and body mass is nearly linear, suggesting their gas exchanger can support resting metabolism across different sizes. However, during maximum exercise, the gas exchanger in larger salmonids struggles to meet increased metabolic demands. Jones and Randall summarize that size limitations for oxygen uptake in fish like tench are set by resting metabolism, while in more active fish like salmonids, they may be set by the demands of active metabolism. Different fish species have varying capacities to increase oxygen uptake during exercise, influenced by their morphometric and physiological characteristics.

In addition to morphometric factors, physiological adjustments play a crucial role in enhancing oxygen uptake during exercise. A key adaptation observed in fish is the significant increase in ventilation volume, a direct response to escalated oxygen demand during activities like sustained swimming or escape responses. By increasing the flow of water over their gills, fish augment the volume of water ventilated, thereby maximizing oxygen extraction. This enhanced ventilation ensures a steady oxygen supply to tissues, vital in environments where oxygen levels may be variable or limited. Hemoglobin's role in oxygen transport becomes increasingly important during heightened activity, facilitating efficient oxygen transport from gills to muscles. The increased ventilation and effective oxygen transport by hemoglobin underscore the fish's ability to modulate its respiratory system in response to varying metabolic demands. This balance between energy expenditure and efficient oxygen uptake is critical for sustaining prolonged physical activity and survival in diverse aquatic environments.

Jones and Randall highlight how Brett's (1964) research and subsequent studies with Brett and Glass (1973) made significant contributions to our understanding of exercise physiology in fish, particularly sockeye salmon. Brett discovered that both active and standard oxygen uptake in sockeye salmon were temperature-dependent, with a notable increase in metabolic rate up to 15 °C, beyond which the rate plateaued due to respiratory system limitations in supplying sufficient oxygen. Increasing the water's oxygen concentration by 50% at 20 °C significantly increased active metabolism, indicating that oxygen supply was a limiting factor. Brett and Glass also found that active oxygen uptake in sockeye salmon was largely independent of body size, contrasting with standard metabolism, which is proportional to body weight to the power of 0.78 (i.e., standard metabolism decreases relative to body weight as the fish grows, while active metabolism remains constant). This independence from body size makes active oxygen uptake a valuable and consistent measure of exercise performance in fish. These foundational findings are crucial today, informing current studies on fish physiology related to aquaculture, fisheries management, and ecological research, where understanding energy expenditure and oxygen usage under varying conditions is essential.

Research on oxygen consumption in fish during exercise highlights the complexity of energy conversion under these conditions. Oxygen uptake rates alone may not fully represent total energy expenditure, as anaerobic metabolism contributes significantly during high-intensity activities. Studies by Black et al. (1960, 1962), Connor et al. (1964), Beamish (1968), and Driedzic and Kiceniuk (1976) indicate that at moderate swimming speeds, changes in muscle glycogen and blood lactate levels are minimal, suggesting predominantly aerobic energy metabolism. However, during burst activities, there is a rapid increase in both muscle and blood lactate levels, along with a decrease in muscle glycogen, indicating a shift to anaerobic metabolism. The extent to which anaerobic metabolism contributes to the energy budget during sustained exercise remains debated. Smit et al. (1971) argued that anaerobiosis plays a significant role during sustained swimming in goldfish, while Kutty (1968), based on respiratory quotient (RQ) determinations, did not find evidence of anaerobic metabolism in goldfish and trout during sustained swimming. An initial anaerobic phase at the start of sustained swimming was suggested by a higher mean RQ in the first hour of exercise. As fish approach their critical velocity, anaerobic energy contribution increases, leading to a cumulative oxygen debt, described by Brett (1964). This debt is repaid during the post-exercise recovery period. In tests where velocity is incrementally increased, anaerobic metabolism is present immediately following each increment and throughout the exercise period at speeds close to the fish's critical velocity. This understanding is crucial in current research, providing insights into physiological responses during different types of exercise, aiding in designing appropriate exercise regimes in aquaculture, understanding fish endurance limits in natural settings, and assessing the impact of environmental stressors on fish metabolism. The balance between aerobic and anaerobic metabolism influences fish behavior, growth, and survival.

6 Swimming muscles

The application of electromyography (EMG) in fish exercise physiology, as detailed in the chapter, has been a pivotal development. EMG allows for the direct measurement of muscle activity, providing insights into the muscular workload during various forms of exercise (Rome et al., 1990). This technique has been instrumental in understanding the balance between energy expenditure and locomotor activity, offering a window into the metabolic strategies fish employ during sustained physical activity (Jayne and Lauder, 1995).

Fatigue in fish during sustained exercise is influenced by various factors, including muscle glycogen depletion and metabolic by-product accumulation (Brett, 1964). The mechanisms of fatigue are complex and can vary significantly among species and types of activity. Examining respiratory adjustments during exercise has shed light on the intricate mechanisms fish use to meet increased oxygen demands. The role of hemoglobin in oxygen transport and the adjustments in gill ventilation have been key areas of study (Perry and Gilmour, 2006). These insights have been crucial in understanding how fish respond to environmental challenges such as hypoxia (Randall and Daxboeck, 1984). Modern research, employing advanced imaging and molecular techniques, provides in-depth understanding of the biochemical pathways leading to fatigue in fish. These methods enable the observation of real-time changes in muscle tissues and blood chemistry during exercise. Investigating genetic factors that influence fatigue resistance is particularly promising, as it could identify specific genes or molecular pathways to enhance performance in aquaculture species. Additionally, understanding these mechanisms is vital for conservation, especially for migratory species. For example, transcriptomics studies have been instrumental in revealing exercise-induced changes in muscle tissue gene expression, offering new perspectives on fish physiology (Palstra and Planas, 2011).

7 Cardiovascular dynamics in fish during exercise

In addition to the respiratory adaptations, the cardiovascular system plays a crucial role in supporting exercise in fish. As Jones and Randall highlighted, arterial blood pressure and total peripheral resistance (TPR) undergo significant changes during exercise. This is echoed in the findings of Johansen et al. (1966), who observed that arterial blood pressure increases in teleosts during exercise, with ventral aortic pressure rising markedly in the early part of a bout of activity. Kiceniuk and Jones (1977) further elaborated on these changes, noting that the magnitude of the increase in mean arterial blood pressure is consistent, regardless of whether the fish starts swimming from rest or during an incremental velocity test. This suggests that the cardiovascular response may be more related to disturbance and cardiac overcompensation than to exercise stress, *per se*. The role of venous pressure and venous return during exercise is equally critical. The increase in venous pressure, particularly in the subintestinal vein during moderate swimming speeds, as reported by Stevens and Randall (1967), indicates hepatic venomotor activity and a potential redistribution of blood away from visceral regions during exercise. Kiceniuk and Jones (1977) observed that while dorsal aortic pressure changes are smaller than ventral aortic pressure changes, they still play a significant role in the overall cardiovascular response to exercise. These cardiovascular adjustments, including the changes in arterial and venous pressures and the differential responses in the gill and systemic circulations, highlight the complex interplay of physiological systems during exercise in fish. The ability to maintain arterial blood pressure against varying levels of TPR, as well as the efficient management of venous return, underscores the sophistication of the fish cardiovascular system in responding to the demands of exercise.

8 Exercise and the circulatory system

Having explored the specific dynamics of arterial and venous pressures during exercise, it becomes clear that the circulatory system in fish, encompassing heart function and blood flow, plays a pivotal role in supporting sustained exercise. Key adjustments during exercise include changes in heart rate, stroke volume, and blood pressure, which are essential for meeting the increased metabolic demands. Beyond these adjustments, the circulatory system is intricately involved in the transport of oxygen from the gills to the tissues. This process is elegantly described by the Fick equation, which has become a staple in fish physiology and physiological research in general, serving as a foundational concept for students and researchers alike, spanning those just beginning their research careers to seasoned scientists. The Fick equation states that the rate of oxygen consumption is the product of cardiac output and the difference in oxygen content between arterial and venous blood.

$$\mathrm{VO_2} = Q(\mathrm{CaO_2} - \mathrm{CvO_2})$$

where:

- $\mathrm{VO_2}$ is the rate of oxygen consumption (uptake).
- Q is the cardiac output, which is the volume of blood pumped by the heart per minute.
- $\mathrm{CaO_2}$ is the arterial oxygen content, which is the amount of oxygen carried in the blood leaving the heart and going to the tissues.

- CvO_2 is the venous oxygen content, which is the amount of oxygen remaining in the blood after it has passed through the tissues.

This equation not only highlights the critical role of the cardiovascular system in ensuring efficient oxygen delivery to meet the heightened metabolic demands during exercise but also serves as a cornerstone in the education and research of fish physiology. Indeed, focusing on the circulatory system's response to exercise has led to a deeper understanding of cardiovascular physiology in fish.

The discovery of the heart's remarkable plasticity and its ability to adapt to varying exercise demands represents a significant advancement in the field (Anttila et al., 2014). This research has shed light on how fish maintain physiological balance during periods of increased activity and stress (Steinhausen et al., 2008). Modern research, leveraging telemetry and biologging technologies, has enabled the study of these circulatory adjustments in natural environments, providing invaluable insights into how fish respond to various environmental stressors (Farrell et al., 2009). Looking ahead, future research could pivot toward assessing the impact of environmental stressors on circulatory health. This focus is crucial for conservation efforts and for predicting the resilience of fish populations in the face of ecological changes (McKenzie et al., 2007). Such studies are not only pivotal for ecological and conservation strategies but also offer broader implications for understanding vertebrate physiology under environmental stress.

9 Integrating advanced technologies in fish physiology research

The integration of molecular biology and telemetry in studying fish in natural environments is paving the way for more comprehensive ecological and conservation strategies. For example, transcriptomics and genomics have allowed for a more detailed understanding of the genetic and cellular mechanisms underlying fish physiology (Gracey et al., 2004). The integration of telemetry in studying fish in natural environments is paving the way for more comprehensive ecological and conservation strategies (Cooke et al., 2004). Advancements in fish physiology research not only pave the way for future academic studies but also hold significant practical applications. This evolving body of work is essential in shaping sustainable fisheries management and enhancing aquaculture practices, while simultaneously deepening our understanding of the broader ecological impacts stemming from physiological adaptations in fish (Brett, 1995; Cooke et al., 2013, 2016).

10 Concluding thoughts

Reflecting on the past 45 years since the seminal work of Jones and Randall on "The respiratory and circulatory systems during exercise" in *Fish Physiology*, it is evident that this field has undergone significant evolution and expansion. Their foundational framework has not only advanced our understanding of fish physiology but also set the stage for future research directions. Key advancements in the field have been driven by the development of sophisticated methodologies, such as swim flumes, and the integration of molecular biology and telemetry. These tools have enabled precise measurements of fish exercise performance and provided deeper insights into the physiological responses of fish to various stressors. The exploration of cardiovascular and respiratory adaptations during exercise has been particularly illuminating, revealing the remarkable plasticity of these systems in fish.

The research has shown that fish, much like human athletes, undergo complex physiological changes to meet the demands of exercise. These changes, including increased ventilation volume and adjustments in heart rate and blood pressure, are crucial for efficient oxygen delivery and utilization. The role of hemoglobin in oxygen transport and the intricate balance between aerobic and anaerobic metabolism have been key areas of study, offering insights into the endurance and survival strategies of fish.

Looking ahead, the field of fish exercise physiology is poised to address new challenges and questions. The impact of environmental stressors, such as climate change and habitat degradation, on the physiological health of fish populations is an area of growing concern. For example, research on heart rate and cardiac function in Arctic fishes provides critical insights into how rising temperatures affect cold-adapted species. Findings reveal that Arctic char (*Salvelinus alpinus*) exhibit rapid compensatory cardiac plasticity, reducing maximum heart rate (f_{Hmax}) over intermediate temperatures and improving their ability to increase f_{Hmax} during acute warming, which enhances cardiac thermal tolerance (Gilbert et al., 2022b). Further studies demonstrated that Arctic char can adjust their cardiac performance with thermal acclimation, increasing their cardiac heat tolerance significantly with acclimation temperatures of up to 14 °C; although, prolonged exposure to 18 °C proved lethal (Gilbert and Farrell, 2022). Field-based research using a mobile aquatic-research laboratory showed that Arctic char's f_{Hmax} increases with temperature up to a critical point, beyond which it declines and becomes arrhythmic, highlighting the vulnerability of this species to extreme thermal events (Gilbert et al., 2021). Similar rapid cardiac plasticity has been observed in rainbow trout, indicating that such mechanisms might be widespread among fish species to mitigate acute thermal challenges (Gilbert et al., 2022a). This is an area that certainly warrants further investigation.

On a personal note, I had the honor of learning from Jones during the first year of my PhD, before he passed on, and luckily much more time with Randall, not only through my PhD and post-doctoral work, but well into my career as a university professor as well, until his passing in April 2024. Undoubtedly, the legacy of Jones and Randall's work continues to inspire and guide research in fish physiology, and both have left a lasting impression on our field.

Indeed, future research could focus on assessing the resilience of fish to such stressors that will become more frequent and severe into the future and exploring conservation strategies to protect diverse aquatic ecosystems. As we advance our understanding of the complex interplay between the environment and physiological adaptations in fish, we are better equipped to appreciate the intricacies of aquatic life and the challenges it faces in a rapidly changing world.

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