



Review

Perspective – Exercise in fish: 50+ years and going strong[☆]James D. Kieffer^{*}

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ABSTRACT

Swimming in fish has garnered the attention of researchers for more than 50 years. Research has focused on the mechanisms that fish utilize during exercise, fuel use patterns, recovery dynamics and the effects of abiotic and biotic factors on fish exercise physiology. Research direction has been influenced both by technology (e.g., availability of telemetry devices and access to swim flumes) and environmental changes (e.g., global warming and pollution). In addition, researchers have begun to examine the interplay between swimming physiology and behaviour. As part of the 50th Anniversary of Comparative Physiology and Biochemistry, this perspective examines the history of fish exercise research, and some of the individuals who have made significant contributions.

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1. Introduction

Whether it is their incredible ability to deal with high and low temperatures, hypoxia, or their capacity to swim at extremely high speeds, fish have provided researchers with an extremely robust model to study basic physiological processes. As fish utilize various strategies (e.g., behavioural, molecular and physiological) to survive challenging environments, researchers studying the physiology of fish have also developed new methods to study these fascinating

creatures. What researchers did 50 years ago has shaped our current thought, and the questions we ask today will shape how our successors undertake new and exciting research. Many journals, including Comparative Physiology and Biochemistry, have enabled researchers to publish excellent original and review articles on the subject of fish exercise physiology and biochemistry.

Over the past 50+ years, researchers have published a large body of physiological research on swimming and exercise capacities of fish (see Beamish, 1978; Milligan, 1996; Kieffer, 2000; Farrell, 2007). For those working in the field, it is apparent that much of our current knowledge is the result of the initial contributions of several Canadian scientists. In this regard, I will highlight how these researchers have contributed to the fields of fish exercise physiology and performance. Since there are many reviews on this subject (Wood, 1991; Milligan,

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1996; Kieffer, 2000), my objectives are not to provide an extensive analysis, but rather to highlight some of the major findings/directions over the past 50+ years. Moreover, I will describe general areas of research, rather than provide a quantitative approach to the study of fish exercise. I end the perspective by suggesting some areas that require further study.

1.1. Types of swimming

The past 50–60 years have been fruitful with regard to fish swimming physiology and performance studies. Several comprehensive reviews on this subject have been published in this journal (Milligan, 1996; Davison, 1997; Kieffer, 2000; Plaut, 2001; Bernal et al., 2001; Nelson et al., 2002) and elsewhere (e.g., Wood, 1991; Randall and Brauner, 1991; McKenzie et al., 2007) for several groups of fish. For various practical (e.g., availability of various sizes of fish, easy to hold in the lab) and physiological reasons (e.g., considered high performance fish), most of the research on the swimming capacity and performance in fish has focused on salmonids (Moyes and West, 1995), although this has changed over the past couple of decades. Levels of swimming performance in fish are traditionally defined in terms of duration of swimming and intensity in which the fish swims (reviewed in Beamish, 1978). Researchers have categorized swimming in fish into three broad categories: sustained, prolonged, and burst-type swimming (see Brett, 1964; Beamish, 1978; Hammer, 1995; Plaut, 2001, for details). Aerobic metabolism powers sustained exercise, and includes those speeds maintained for long periods of time (typically greater than 200 min) without resulting in muscular fatigue (Beamish, 1978). Prolonged exercise lasts between two and 200 min and, depending on the swimming speed, ends in exhaustion. A third type of exercise, intense burst activity, relies almost exclusively on anaerobic metabolism within the white muscle and lasts for short periods of time (typically less than 20 s). This type of exercise typically results in a significant reduction of intracellular energy supplies and in an accumulation of waste products (Kieffer, 2000).

1.2. Early influences

Although several key Canadian researchers laid important groundwork for our understanding of swimming in fish (see below, Black, 1957a,b,c; Brett, 1964), the pioneering work of F.E.J. Fry (1947) “Effects of the Environment on Animal Activity” provided some of the initial framework of how to examine the problem of exercise in fish (scope for activity, for example). In particular, Fry wrote about the importance of controlling factors (namely temperature) and the relationship between “how the animal works” (e.g., metabolism) and “what the organism does” (e.g., activity/ swimming). In his seminal work, Fry also wrote about the importance of previous experience of the organism (e.g., training) in relation to the factor of the environment under consideration.

1.3. The Great Division — pioneers of sustained and exhaustive exercise research in fish

The importance of Fry's work on temperature and metabolism cannot be overstated, and this early work paved the way for future work on both exhaustive (anaerobic) and sustained (aerobic) exercise. The research of two eminent fish physiologists, J. R. Brett and E. C. Black, emerged several years following the publication of Fry's seminal work. Black worked extensively on lactic acid production in fishes, most notably salmonids (Black, 1955, 1957a,b,c) and Brett's work focused on swimming and aerobic metabolism (Brett, 1964). Around that time, P.W. Hochachka began working on the effect of training on “oxygen debt” and metabolic fuels in trout (Hochachka, 1961).

Brett (1964) focused on the metabolic costs of swimming in fish, with a strong emphasis on temperature relationships and aerobic metabolism in salmon (reviewed in Brett, 1995). The development of the Brett swim flume and the theory behind its use would prove pivotal to the development of the critical swimming test (UCrit test; see below). The roadmaps that Brett established have become instrumental in setting a direction for much of the work of others, including Hockachka, Stevens, Wood, Jones, Randall, Boutilier, Kolok, Nelson, Claireaux, Steffensen, Tufts and Farrell and all of their students and collaborators (the list could fill many pages!).

1.4. The importance of swimming tests: what we know and where we are headed

Much of our understanding of the aerobic swimming capacity of fish has resulted from the development of swim flumes/respirometers. Although swim flumes were used by others (e.g., Blazka et al., 1960), Brett developed some of the initial swimming tests used to assess aerobic swimming capacities in fish (Brett, 1964). The “critical swimming test” (UCrit) is still the tool used most widely by researchers to evaluate aerobic swimming performance in fish. This test measures the highest sustainable swimming speed achieved by a fish. Various reviews found within this journal (e.g., Hammer, 1995; Plaut, 2001) and elsewhere (e.g., Beamish, 1978) have described the methodology/history of this test. Various researchers have critically evaluated the methodology involved with this test (e.g., magnitude and duration of velocity increments used in the test, repeatability of individuals, Kolok, 1992; Plaut, 2001; Hammer, 1995; Kolok, 1999) and its relevance beyond physiological study (Plaut, 2001). Despite some methodological considerations, UCrit tests remain popular as a means of evaluating the effects of different factors (e.g., fish size, temperature, salinity, dissolved gases and pollutants; see Beamish, 1978; Randall and Brauner, 1991; Kieffer and Cooke, 2009) on fish swimming ability and metabolic costs of swimming at UCrit. A large literature exists on species-specific UCrits in fish (e.g., Beamish, 1978; Peake, 2004; McKenzie et al., 2007; Kieffer and Cooke, 2009), which has often tempted researchers to categorize fish performance based on UCrit values.

Although many studies have utilized critical swimming tests to assess performance, Farrell (2008) has contributed to some of our most recent and thorough understanding of the relationship(s) between critical swimming speeds, temperature, metabolic costs and cardiac function in fish (reviewed in Farrell, 1996, 2007, 2008). Embedded within this research has been the investigation of repeat performance in fish (Jain et al., 1998; Farrell et al., 1998; MacNutt et al., 2004; Peake and Farrell, 2004). That is, whether or not fish can repeat a critical swimming test following a brief rest between tests (i.e., UCrit vs. UCrit2). Various studies by A.P. Farrell's group have identified some of the rate-limiting factors (e.g., high temperature) on the recovery processes following aerobic swimming. Specifically, their work confirmed that for some salmonid fish a recovery period of 40 min between UCrit tests is sufficient for routine oxygen consumption levels to return to normal. Originally, it was suggested that a longer period (i.e., 4 h) was required (Brett, 1964) for full metabolic recovery between UCrit tests.

1.5. Swimming tests and validation — what's new?

While the UCrit test continues to be a popular test used by physiologists and ecologists interested in fish exercise capabilities, researchers have modified the test over recent years (e.g., ramp-UCrit test — Jain et al., 1997). In particular, some researchers have challenged whether the UCrit test is valid, in part, because fish may never swim at their UCrit for an extended period under natural conditions (reviewed in Plaut, 2001). In addition, researchers have focused on the limitations of swim flumes (to measure UCrit)

Table 1
Brief summary of published research on various aspects of exhaustive exercise in fish.

Year Grouping	Topic Area	Representative References
1950s–1970s	Hematology and Lactate Dynamics	(Black, 1955, 1957a,b,c; Black et al., 1962, 1966)
	Training Effects	Hochachka (1961)
	Blood Flow Effects	Stevens (1968)
	Intermittent Exercise	Stevens and Black (1966)
1980s–2000s	Exercise Training	(Lackner et al., 1988; Pearson et al., 1990)
	Lactate releasers versus non-releasers	(Milligan and Wood, 1986a,b; Milligan and McDonald, 1988)
	Effects of abiotic and biotic factors on recovery	(Goolish, 1989; Dalla et al., 1989; Tang and Boutillier, 1991; Ferguson et al., 1993; Wilkie et al., 1996; McDonald et al., 1998; Kieffer, 2000 (review); Galloway and Kieffer, 2003; Clutterham et al., 2004)
	Role of gill in correcting acid base disturbances (models)	(Holeton et al., 1983; Milligan and Wood, 1986a; Wood, 1988; Kieffer and Tufts, 1996)
	Role of Hormones on recovery	(Milligan and Wood, 1986a,b; Wood et al., 1990; Pagnotta et al., 1994; Milligan, 1996 (review); Eros and Milligan, 1996; Milligan et al., 2000; Milligan, 2003;)
	Post-exercise oxygen consumption	(Scarabello et al., 1991; Scarabello et al., 1992; Lee et al., 2003)
	Integration of response (e.g., acid–base, ion, metabolite)	(Dobson and Hochachka, 1987; Wood, 1991 (review); Arthur et al., 1992; Schulte et al., 1992; Wang et al., 1994; Moyes and West, 1995 (review))
	Field Testing (catch and release angling)	(Booth et al., 1995; Kieffer et al., 1995; Wilkie et al., 1996; Suski et al., 2003)
	Metabolic Fuel use and Recovery	(Wang et al., 1994; Milligan, 1997; Richards et al., 2002)
	Cardiovascular Effects	Reviewed in Farrell, 2007
	Regulation of gas transport	(Milligan and Wood, 1987; Tufts et al., 1991)
	Link between behaviour and recovery	(Milligan et al., 2000; Farrell et al., 2001; Peake and Farrell, 2004 ; Suski et al., 2007; Clutterham et al., 2004; Lee-Jenkins et al., 2007)
	Applied Physiology and Conservation Physiology	Wikelski and Cooke (2006)

(reviewed in Plaut, 2001) and others have recently suggested that the capacity of fish to swim in a flume involves a large behavioural component (McFarlane and McDonald, 2002; Peake and Farrell, 2006; Peake, 2008) that could affect the final value for UCrit. Nelson et al. (2002) recently developed additional tests (e.g., sprint performance and acceleration tests) that may better reflect the diversity of fish swimming styles and how other types of swimming performance relate to UCrit; in particular, these tests emphasize the ecological and evolutionary implications of variance in aquatic locomotory performance. Also, swim flumes may constrain/confine fish when they are forced to maintain position against a water speed that is too high to be efficiently maintained using a steady locomotory gait, and too low to be held using an unsteady (i.e., burst and glide) type gait (for details, see Peake and Farrell, 2006; Tudorache et al., 2007, and Peake, 2008). Consequently, UCrit tests may underestimate the true swimming capacity of fish. Peake (2008) suggests that by focusing on gait transition and allowing fish to swim volitionally, the behavioral component may be reduced and proper swimming performance can be evaluated.

Although the physiological value of the UCrit test has been validated (i.e., they are repeatable among individuals, easy to conduct, the effects of abiotic and biotic factors can be assessed), some researchers suggest that the utility of the test may be compromised when one wishes to draw ecological or evolutionary inference (Reidy et al., 2000). Future work should address the relationship between fish behavior (e.g., gait transition) and swimming performance in fish. Work should also compare swimming capacity under conditions that are more natural and across populations (Hasler et al., 2009).

2. Physiology and biochemistry of exhaustive exercise in fish

With respect to swimming activity, fish swim mostly aerobically (i.e., sustained and prolonged swimming). Despite this general observation, much of our understanding of swimming metabolism has been the result of research done on burst, exhaustive exercise (Wood, 1991). Wood (1991) describes the common methods for producing exhaustion in fish.

Over the past 50 years, many important “benchmarks” have been established with respect to exhaustive exercise in fish. Early research by Black (see Table 1; Black, 1957a,b,c; Black et al., 1962) and

Hochachka (1961) and their colleagues have helped identify the physiological response to exercise, the time course for recovery and the biochemical aspects of exhaustive exercise (see Wood, 1991, for a review). Several comprehensive reviews are published in this journal and elsewhere on the physiological and biochemical aspects of exhaustive exercise in fish (Wood and Perry, 1985; Wood, 1991; Moyes and West, 1995; Milligan, 1996; Kieffer, 2000). In particular, Wood (1991) and Milligan (1996) provide excellent accounts of the ion, acid–base, metabolic and hormonal effects of exhaustive exercise in fish. Selected examples and references are also included in Table 1.

Unlike aerobic exercise, the bulk of the work on exhaustive exercise in fish has taken place over the past 30 years; significant advances occurred in the 1980s, especially inter-specific research comparing high performance swimmers to sluggish fish (lactate non-releasers; Milligan and Wood 1986a,b). Focus of the 1990s was on intra-specific comparisons (variation), mechanisms of recovery and the importance of other less-studied metabolic fuels (i.e., lipids) on the physiological recovery process (see Table 1). During the current decade, research has focused on the connection between behavior and physiology (Gilmour et al., 2005). From a comparative perspective, most research on exhaustive exercise continues to utilize the salmonid model, but recent reviews on tuna (Arthur et al., 1992; Bernal et al., 2001), sharks (Bernal et al., 2001) and centrarchids (Kieffer and Cooke, 2009) have identified characteristics of exercise and recovery that extend beyond the salmonid model.

3. 1950s and 1960s

Black's (1955) early research focused on hemoglobin dynamics in various species of fish, but his later work on post-exercise lactate dynamics in salmon may be considered his largest contribution to exercise physiology in fish (Black, 1957a,b,c; Stevens and Black, 1966). Black was among the first researchers to describe the pattern of lactate efflux from muscle into the blood of fish following strenuous/exhaustive exercise. This work made it possible for others to: (i) “dissect” the rate limiting steps (reviewed in Wood, 1991; Milligan, 1996; Kieffer, 2000), (ii) study the mechanisms for lactate release (Milligan and Wood, 1986a,b; Wang et al., 1994), (iii) investigate how metabolic pathways are integrated (e.g., role of hormones, oxygen consumption; Wood and Perry, 1985; Schulte et al., 1992; Moyes and

West, 1995) and (iv) understand the metabolic fuel patterns during recovery from exercise (Wang et al., 1994; Richards et al., 2002). Black's early work also had a clear application; it was concerned with mortality in fish following exhaustion, a topic that has not yet been addressed fully (Wood et al., 1983; Kieffer et al., 2002). Recent work, largely based on Black's detailed studies, has focused on a new and exciting field of conservation physiology (see below).

Although research from the 1950s and 1960s focused largely on salmonids, the 1980s brought to the forefront other fish models. In particular, largemouth bass and species of flounder and sole became useful models, in large part due to the environments (e.g., saline vs. freshwater, stenotherms vs. eurytherms) these fish occupy. Despite this, comparative fish physiologists continue to utilize the salmonid model for exercise studies, and researchers should continue to find alternate fish models.

4. 1980s and 1990s – an explosive period

The 1970s were a relatively quiet time for fish exhaustive exercise studies, but a significant amount of work during the 1980s (in particular) and 1990s began to investigate the mechanisms involved in the recovery process. Because the speed of recovery from exercise is slow in fish (Wood, 1991), many studies have examined the impact of abiotic and biotic factors on recovery processes (reviewed by Wood, 1991; Milligan, 1996; Kieffer, 2000).

4.1. Exhaustive exercise: significant contributions

Both Wood's (see Wood, 1991) and Hochacka's (Dobson and Hochachka, 1987) labs became known for their work on exhaustive exercise physiology in fish during this time. Each lab had slightly different foci, but each uncovered interesting and relevant findings that were complementary. Wood's lab focused on lactate dynamics between ecologically different species of fish (flounder vs. trout; lactate non-releasers vs. releasers) and was interested in pH regulation and recovery of lactate (Milligan and Wood, 1986a,b). In addition, Wood's group investigated the role of catecholamines on the metabolic costs (e.g., EPOC) associated with recovery (e.g., Wood, 1991; Scarabello et al., 1991, 1992) and the importance of the kidney and gill in the removal of metabolic protons that accompanied exhaustive exercise (reviewed in Wood, 1988). Other major contributions by Wang et al. (1994) to exhaustive exercise include the mechanisms responsible for lactate and proton dynamics and the role of other fuels, such as lipids, involved in the exercise recovery process. Further work by Richards et al. (2002) supported earlier hypotheses (e.g., Wang et al., 1994) by showing that intra- and extra-muscular lipids are oxidized by the white muscle to fuel the generation of ATP, phosphocreatine and glycogen.

Among other areas of study, Hochachka's lab focused on the bioenergetics of exercise across a full range of biological levels (from enzymes, pathways, and mitochondria, to isolated muscle fibers, perfused hearts, and whole animals). Research focused on the many integrative mechanisms of biochemical control following exercise (Dobson and Hochachka, 1987; reviewed in Moyes and West, 1995).

A third significant contribution in the 1990s to fish exhaustive exercise physiology was the role of cortisol on the post-exercise recovery dynamics in fish. This work has uncovered important biological and practical aspects of exercise recovery in fish. In addition to advancing our understanding of the link between cortisol and recovery, Milligan and her collaborators (e.g., Milligan, 2003; Frolow and Milligan, 2004) adopted several novel techniques (e.g., use of membrane vesicles, pharmacological agents and radioactively labeled compounds) to address the movements of metabolites across the muscle membrane.

4.2. Applied exercise physiology

During the 1990s a divergence of research related to exhaustive exercise in fish occurred. Several researchers began to focus on exercise-induced changes under more natural conditions, a trend that still is attributed to the earlier work of Black (e.g., Black, 1955), who was interested in post-exercise mortality. During the 1990s, researchers applied exercise theory to practical situations, such as commercial fishing and recreational angling. This type of work initially started in the 1980s, but the numbers of research papers began to peak during the 1990s and early 2000s. Some of the earliest work on catch and release focused on salmonids (Booth et al., 1995; Wilkie et al., 1996) but the mid-1990s and early 2000s introduced a relatively new model, the Centrarchidae (e.g., bass and sunfish; reviewed in Cooke et al., 2002; Kieffer and Cooke, 2009). The major contribution of many of these applied studies was to identify the importance of biotic (body size, stage of migration, exercise time) and abiotic (hypoxia, temperature) factors on post-exercise physiology (Table 1).

5. 2000 and beyond

While several controversial areas still exist (e.g., roles of cortisol and catecholamines; fate of lactate, metabolic changes during the exercise period), there appears to be a noticeable change in research direction. Current research is integrative, however, it focuses on the inter-relationships between behaviour and exercise. Traditionally, behaviour and physiology were two separate areas of study, with the majority of researchers focusing on one or the other. Recent work, some outlined below, demonstrates the growing interest in understanding the physiological mechanisms underlying various behaviours, such as swimming (Gilmour et al., 2005). Milligan (1996) represents one of the major landmark papers. Milligan (Milligan, 1996; Milligan et al., 2000) has been working on the effects of post-exercise elevations of cortisol on the fate of lactate in fish. There is strong evidence that the elevation of plasma cortisol levels associated with the exhaustive exercise delays the restoration of metabolite and acid–base status to pre-exercise levels (Pagnotta et al., 1994; Eros and Milligan, 1996). Recently, Milligan et al. (2000) have made the connection between post-exercise aerobic swimming behaviour, cortisol levels and metabolic recovery in rainbow trout. Briefly, they found that fish allowed to swim aerobically during recovery from exhaustive exercise had lower cortisol levels and recovered their post-exercise lactate loads about 2 times faster than fish held in still water. These studies have been replicated for Pacific salmon (Farrell et al., 2001) and largemouth bass (Suski et al., 2007).

The research of Milligan et al. (2000) has triggered a number of recent studies which have assessed the importance of behaviour on the physiological response to exercise (Farrell et al., 2001; Peake and Farrell, 2006; Veiseth et al., 2006; Lee-Jenkins et al., 2007). Two notable examples include the work by Peake and Farrell (2006) and Lee-Jenkins et al. (2007). In their paper, Peake and Farrell (2006) emphasized the importance of assessing gait transitions (i.e., between steady and unsteady swimming behaviour) in understanding the metabolic fuel use patterns during high-speed swimming in fish. Lee-Jenkins et al. (2007) studied the recovery of locomotory activity in exhausted juvenile rainbow trout. The overall conclusions from this experiment shows that recovery processes are affected by ontogeny and/or size of fish, and thus, the reduction in burst swimming of juvenile trout makes younger/smaller fish more vulnerable to aquatic predators (Lee-Jenkins et al., 2007).

Critically assessing the relationship between behaviour and the post-exercise physiological response (at the individual and population level) requires the development of suitable physiological tools. Over the past 10–20 years, technology has provided researchers with numerous (albeit expensive) telemetry devices to track fish during

migration (Hinch et al., 1996; Cooke et al., 2004). Telemetry has enabled scientists to both track fish (e.g., where fish go) and estimate the energy budgets over time (e.g., during migration). This area of research is critical to our understanding of the physiological aspects of exercise, particularly under field conditions. Donaldson et al. (2008) reviews the current literature on the usefulness of utilizing biotelemetry for applied fisheries questions (e.g., catch and release).

6. Where do we go from here?

Research from the last 50–60 years has moved forward the field of fish exercise physiology. There have been significant advances in the development of tools (e.g., swim flumes, telemetry equipment) and various methodologies to investigate the ion, acid-base and metabolite status of fish.

In many respects, researchers have only scratched the surface of our understanding of swimming capacities of fish. In particular, most work on exercise physiology in fish has been conducted on salmonids; other fish species, such as polar fish and tropical fish have largely been ignored. Research has now begun to investigate the molecular and genetic aspects of exercise in fish. This area will undoubtedly be popular as new fish models become available. Other cross-disciplinary approaches have included the impact of behaviour on the physiological response to exercise. These approaches will uncover multiple new and exciting research directions (Gilmour et al., 2005).

Much of our understanding about exercise in fish has resulted from experiments conducted under laboratory conditions. This approach is especially important if one is trying to uncover physiological mechanisms. Examining ecologically relevant scenarios (e.g., increases in temperature, CO₂, salinity) has been the focus of more recent studies (see Portner and Farrell, 2008, for an example). Modern advances in gas measuring devices, behavior tracking software, and automated control (e.g., of gases, temperature) will allow laboratory researchers to better test hypotheses that focus on effects of climate change on exercise metabolism in fish. Advances in technology (e.g., telemetry) have allowed researchers to test hypotheses under field conditions. Using the combined laboratory and field based approaches will enable fish physiologists to increase their understanding of the effects of larger-scale environmental issues (see Portner and Farrell, 2008).

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