



SYMPOSIUM

Ecology of Exercise in Wild Fish: Integrating Concepts of Individual Physiological Capacity, Behavior, and Fitness Through Diverse Case Studies

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Synopsis Wild animals maximize fitness through certain behaviors (e.g., foraging, mating, predator avoidance) that incur metabolic costs and often require high levels of locomotor activity. Consequently, the ability of animals to achieve high fitness often relies on their physiological capacity for exercise (aerobic scope) and/or their ability to acquire and utilize energy judiciously. Here, we explore how environmental factors and physiological limitations influence exercise and metabolism in fish while foraging, migrating to spawning grounds, and providing parental care. We do so with three case studies that use a number of approaches to studying exercise in wild fish using biologging and biotelemetry platforms. Bonefish (*Albula vulpes*) selectively use shallow water tropical marine environments to forage when temperatures are near optimal for aerobic scope and exercise capacity. Bonefish energy expenditure at upper thermal extremes is maximal while activity levels diminish, likely caused by reduced aerobic scope. Pacific salmon (*Oncorhynchus* spp.) reproductive migrations frequently involve passage through hydraulically challenging areas, and their ability to successfully pass these regions is constrained by their physiological capacity for exercise. Aerobic scope and swim performance are correlated with migration difficulty among sockeye salmon (*O. nerka*) populations; however, depletion of endogenous energy stores can also limit migration success. In another example, male smallmouth bass (*Micropterus dolomieu*) allocate a significant amount of energy to nest-guarding behaviors to protect their developing brood. Smallmouth bass body size, endogenous energy reserves, and physiological state influence nest-guarding behaviors and reproductive success. We suggest that in some scenarios (e.g., bonefish foraging, Pacific salmon dam passage) metabolic capacity for exercise may be the strongest determinant of biological fitness, while in others (e.g., long distance salmon migration, smallmouth bass parental care) energy stores may be more important. Interactions among environmental and ecological factors, fish behavior, and fish physiology offer important avenues of mechanistic inquiry to explain ecological dynamics and demonstrate how exercise is fundamental to the ecology of fish.

Introduction

Animals are presented with numerous challenges throughout their lifetime that may limit their biological fitness (i.e., survival and the production of viable offspring). On a daily basis, animals must acquire energy from the environment (via foraging) at a greater rate than energy that is expended (via respiration, digestion, and locomotion) for allocation to somatic growth and gamete development (Kleiber 1975; Tytler and Calow 1985). Optimal foraging is challenging, especially considering animals are confronted with additional tasks such as avoiding predators (Milinski and Heller 1978; Lind and Cresswell 2005). In some cases, animals also undertake physiologically challenging migrations to foraging or mating locations (Farrell et al. 2008; Milner-Gulland et al. 2011), or expend significant amounts of energy raising and protecting their young (Clutton-Brock 1991; Smith and Wootton 1995). These behaviors often involve intense physical exercise, which can push animals to their maximal metabolic capacities. Therefore, in some scenarios, the physiological capacity for animals to exercise is an important aspect of their biological fitness (Arnold 1983; Robson and Miles 2000; Le Galliard et al. 2004). In other scenarios, exercise must be sustained over long periods of time when energy intake is limited or non-existent. Thus, the amount and judicious use of energy reserves may be more important to maximize biological fitness (Marden and Rollins 1994; Shepard et al. 2013).

Exercise in vertebrates is fueled primarily by aerobic respiration, which requires oxygen that is attained from the environment (Kleiber 1975). Aerobic scope (i.e., the difference between resting and maximal oxygen consumption rates), therefore, represents the capacity for exercise and is often related to whole animal performance and fitness (Fry 1971; Bishop 1999; Farrell et al. 2008). Aerobic scope offers a potential mechanism to explain why animal populations sustain in some environments and not others (Gannon et al. 2014), and how ecological and anthropogenic factors influence animal behavior and fitness (e.g., in the context of climate change; Clark et al. 2013). However, support for this hypothesis is equivocal (Clark et al. 2013; Lefevre 2016), suggesting aerobic scope is not always relevant to biological fitness, especially in animals with lifestyles that preclude the need for extreme exercise.

If aerobic scope is the primary factor influencing biological fitness, we would expect it to be very high in all animals due to natural selection. However, some animals rarely have to exercise maximally and exercise also incurs energetic costs. Optimal

allocation of energy is often a key factor in biological fitness (Tytler and Calow 1985; Brown et al. 2004). Animals that acquire energy more efficiently via foraging (e.g., consuming more food or food with higher energy density; reducing search and prey handling time) have more to allocate to locomotor activity, growth, and reproduction (Pyke 1984). Natural selection also appears to favor animals that move through the environment with energetic efficiency (Priede 1977; Shepard et al. 2013). Energy reserves are also highly relevant in scenarios where energetically costly behaviors are required, such as mating contests (Marden and Rollins 1994) or long-distance migrations (Sandberg and Moore 1996).

Exercise seems to play important but variable roles in the lives of wild animals, with implications for biological fitness. Yet, relatively little is known about how environmental and ecological factors place physiological constraints on exercise in wild fish, especially in the context of fitness-enhancing activities. Here, in three case studies, we explore how environmental factors interact with physiological capacity to influence the behavior of diverse fish species during fitness-related activities. Our three case studies employ various biologging and biotelemetry techniques to study fish behavior and physiology in the wild (see Cooke et al. 2016 for more discussion of approaches). While it is challenging to measure true biological fitness in wild animals, especially fish, we focus on how ecological factors impose physiological challenges to fishes during physically demanding fitness-related activities including foraging, migration to spawning grounds and parental care.

Case Study 1: Bonefish foraging

Water temperature is one of the most important factors influencing fish metabolism, with implications for scope for activity, animal performance, and biological fitness (Fry 1947; Farrell et al. 2008). There is increasing evidence that aerobic scope in high performance fishes is tightly linked with the thermal regime of their environment (Eliason et al. 2011). Consequently, there are growing concerns that climate change will increase temperatures outside the optimal range of local fish populations (Clark et al. 2013; Muñoz et al. 2015). Tropical fish may be especially vulnerable to increases in water temperature because these species are adapted to live in thermally stable environments (Huey and Hertz 1984; Tewksbury et al. 2008). Further, there is particular concern that increasing water temperatures will

reduce aerobic scope in these species, causing reductions in fitness and population declines (Nilsson et al. 2009).

Bonefish (*Albula vulpes*) occupy diverse habitats across expansive regions of the tropical and subtropical Caribbean Sea and Western Atlantic Ocean (Alexander 1961; Wallace 2014). The bonefish is an interesting model for exploring how temperature influences foraging behavior and activity because individuals often move with tides into shallow, thermally dynamic flats to feed on invertebrates and small fishes (Colton and Alevizon 1983a; Crabtree et al. 1998; Humston et al. 2005). Consequently, increasing temperatures in these shallow water flats due to climate change may limit access to important foraging habitats for bonefish due to thermal exclusion (Murchie et al. 2013; Brownscombe et al. 2017). Given the extreme thermal regime of these environments, we hypothesized that bonefish selectively use these shallow water foraging habitats at temperatures that correspond with maximal aerobic scope.

To explore how temperature influences bonefish foraging activity (Fig. 1) on shallow, thermally dynamic flats habitats, Brownscombe et al. (2017) and Nowell et al. (2015) calibrated acoustic accelerometer transmitters (model V13AP, 35 s transmission delay, ± 3.43 g acceleration range, 5 Hz sampling frequency; Vemco, Bedford, Nova Scotia) to quantify activity and estimate metabolic rates ($\text{mg O}_2 \text{ min}^{-1} \text{ kg}^{-1}$). Brownscombe et al. (2017) deployed accelerometer transmitters in wild bonefish ($n = 10$, 52.1 ± 6.1 cm; mean \pm SD; 41–60 cm range) on a fringing reef flat in tropical Culebra, Puerto Rico (18.2966°N , -65.2500°W) and tracked tagged fish using a fine-scale acoustic telemetry array (i.e., Vemco Positioning System, VPS) consisting of 25 VR2W receivers (Vemco), providing precise, two-dimensional estimates of bonefish position (1.2 ± 2.2 m) from April 2013 to March 2014. Water temperature was measured hourly with two temperature loggers located strategically to capture temperature variation on the reef flat (see Brownscombe et al. 2017 for more details).

To examine whether bonefish used this shallow water flat selectively based on temperature, we calculated a thermal selection index (TSI), as the normalized frequency of bonefish occurrence minus the normalized frequency of water temperatures in 1°C bins. Bonefish spent a disproportionate amount of time at certain temperatures, between 26°C and 29°C , selecting against both colder and warmer temperatures that were available on the fringing reef in Culebra (Fig. 2). Notably, this selective behavior corresponded with the optimal temperature (T_{opt}) for both critical

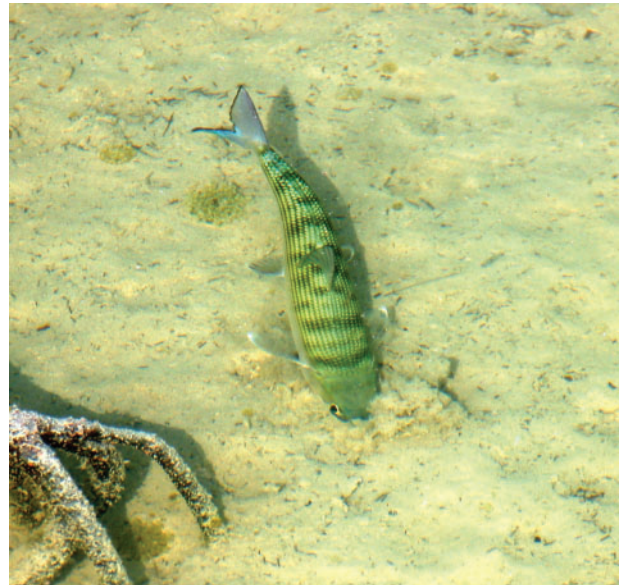


Fig. 1 A bonefish actively foraging in the benthos. Photo Credit: Karen Murchie.

swimming speed (maximum sustained swimming speed; 28.0°C) and aerobic scope (26.7°C), as measured on bonefish in a swim tunnel respirometer in Eleuthera, The Bahamas (Fig. 2). Bonefish swimming activity (acceleration) on reef flats generally increased up to 30°C , but declined steeply thereafter (Fig. 2). This peak in swimming activity was $2\text{--}3^\circ\text{C}$ higher than optimal temperatures for critical swimming speed and aerobic scope for activity, while the decline in activity levels above 30°C followed a similar trajectory to the independent metabolic and swimming performance measures. Importantly, water temperatures in Eleuthera, where measurements of aerobic scope and critical swimming speed were performed, are generally 4°C cooler than in tropical Culebra, where patterns of space use, activity, and energetics were measured (JW Brownscombe, unpublished data). Therefore, peaks in activity at higher water temperatures in Culebra might reflect acclimation to a warmer thermal regime or evolution of different physiological thermal optima. Regardless, this pattern in bonefish activity and metabolic rates provides insight into why bonefish actively select against high water temperatures when there are high energetic costs but little scope for activity to commit to foraging or predator avoidance. Metabolic costs (due to activity and temperature, not considering costs of digestion) at 30°C increased more than two-fold compared to 25°C (Fig. 3). Taken together, as temperatures approach 30°C bonefish metabolic costs increased while aerobic scope decreased, likely causing declines in rates of net energy gain that made foraging on shallow water flats less energetically favorable at upper thermal extremes.

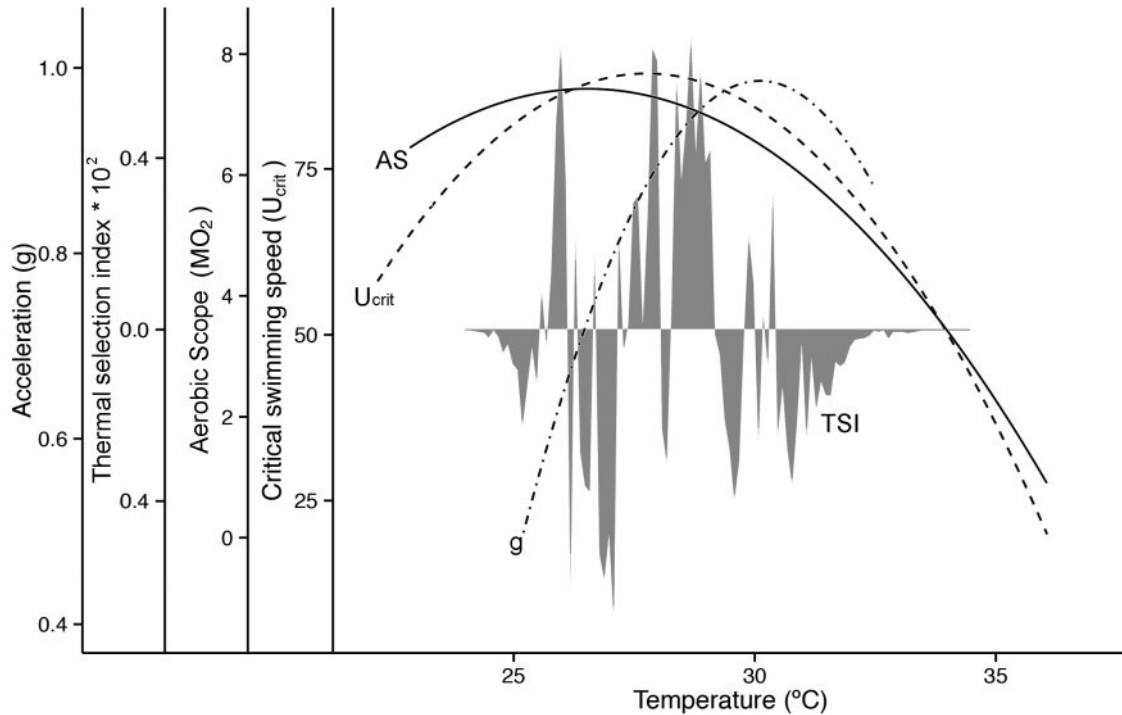


Fig. 2 Relationship between water temperature, bonefish critical swimming speed (U_{crit}) and aerobic scope (maximum metabolic rate minus standard metabolic rate; AS – $\text{mg O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) measured using a swim tunnel respirometer in Eleuthera, The Bahamas, and bonefish thermal selection index (TSI), and mean acceleration levels (g) in foraging habitats in Culebra, Puerto Rico.

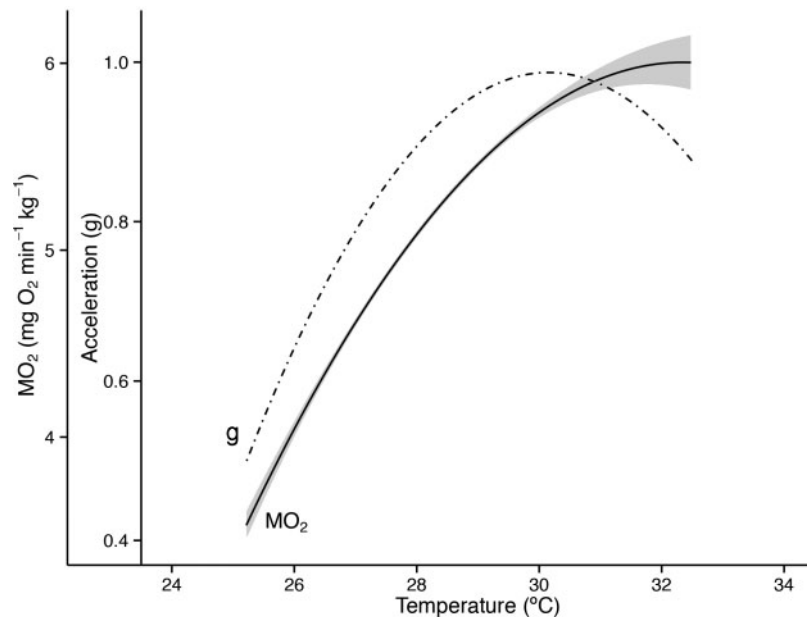


Fig. 3 Relationship between water temperature, bonefish acceleration (g), and estimated oxygen consumption (MO_2 – $\text{mg O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) $\pm 95\%$ CI, on foraging habitats in Culebra, Puerto Rico.

Case Study 2: Pacific salmon migration

Pacific salmon (*Oncorhynchus* spp.) perform a once-in-a-lifetime reproductive migration from oceanic feeding grounds to natal spawning sites. The upriver migration is an energetically challenging feat since

salmon typically cease feeding in the ocean and must fuel swimming and spawning behaviors using endogenous energy stores. Moreover, salmon encounter variable environmental conditions throughout their migration, depending on the timing of

freshwater entry and spawning location (Groot and Margolis 1991). Populations of Fraser River sockeye salmon (*O. nerka*) appear to be locally adapted to their specific migration conditions, where populations with more challenging migrations (i.e., long distance migrations, high river flow) have more somatic energy, fewer eggs, a more stream-lined body shape, greater aerobic and cardiac capacity, larger hearts with a bigger coronary supply, and more energy efficient swimming (Hinch and Rand, 2000; Crossin et al. 2004; Eliason et al. 2011, 2013). In addition, sockeye salmon populations are able to maintain maximal swimming performance and aerobic scope across the typical range of temperatures encountered during their migration (Eliason et al., 2011). Exposure to elevated river flows and to temperatures above the thermal optima for aerobic scope have repeatedly been correlated with high en-route mortality in Pacific salmon, raising significant conservation concerns (Rand et al. 2006; Farrell et al. 2008; Nadeau et al. 2010; Martins et al. 2012).

Pacific salmon use both aerobic and anaerobic swimming to reach their spawning grounds. While anaerobic burst swimming must be used to traverse high river flows, it results in an accumulation of muscle lactate, a reduction in blood pH and oxygen stores, and an imbalance in plasma ions (Scarabello et al. 1992; Gallagher et al. 2001; Steinhausen et al., 2008; Eliason et al. 2013). These physiological disturbances necessitate a prolonged recovery period and additional oxygen uptake required to remove accumulated metabolites and return to homeostasis (termed excess post-exercise oxygen consumption, “EPOC”—Lee et al. 2003). Moreover, failure to reestablish homeostasis can lead to delayed mortality hours or even days later (Priede 1977; Wood et al. 1983). Some populations encounter naturally-occurring, highly turbulent reaches (e.g. Hells Gate, located in the Fraser River ~250 km upstream of the Pacific Ocean) that require anaerobic burst swimming for successful passage (Hinch and Bratty 2000). In addition, some river systems have become regulated by the construction of dams, resulting in fragmented habitats with elevated water flows and temperatures (Caudill et al. 2007). Fish passage structures, such as fishways and fish locks, are designed to mitigate these alterations and allow fish to pass unencumbered; however, some facilities are associated with elevated delayed mortality rates (i.e., mortality in the subsequent days after dam passage; Roscoe et al. 2011). We hypothesized that excessive anaerobic burst swimming related to passing Seton Dam in BC, Canada would be associated with either failed dam passage or delayed mortality in two upstream lakes.

To determine the effects of anaerobic swimming on survival to spawning habitats, Burnett et al. (2014) captured 63 sockeye salmon from the Gates Creek population within the Fraser River Basin downriver of the Seton Dam. Each fish was tagged with a gastrically implanted acoustic accelerometer transmitter (model V13A, 10 Hz sampling frequency; Vemco) and a passive integrated transponder (PIT) tag (32 mm × 3.65 mm, Texas Instruments, Dallas) inserted into the dorsal musculature. Tagged fish were released 200 m downstream of Seton Dam. Swimming activity, behavior, and dam passage was monitored using a fixed acoustic array composed of 18 acoustic receivers (VR2 and VR2W, 69 kHz, Vemco) in the dam tailrace and forebay, as well as three PIT antennas (2.2 m × 0.7 m) in the vertical slot fishway. In addition, survival to spawning habitats was monitored using two VR2W receivers and a three-antenna PIT array installed at the Gates Creek artificial spawning channel.

Tagged salmon had to swim at speeds exceeding the aerobic threshold (i.e., >80% of U_{crit} , as determined by Lee et al., 2003) through fishway attraction flows (Figure 4D) to reach the fishway entrance at Seton Dam (Pon et al. 2009; Burnett et al. 2014). Notably, the amount of anaerobic swimming performed by an individual fish had a positive relationship with dam passage success (Fig. 4A). Excessive anaerobic swimming had a carryover effect on upstream survival. In other words, individuals that spent more time swimming anaerobically in the dam tailrace were less likely to reach spawning grounds (Fig. 4B). Finally, high water temperature was negatively correlated with successful dam passage (Fig. 4C; see Burnett et al. 2014 for more details on probability estimates).

Overall this body of work highlights the potential for carryover effects (see O'Connor et al. 2014) from traversing hydraulically challenging reaches and provides a physiological mechanism for delayed mortality. Females swam with greater anaerobic effort compared to males, which may in part explain why mortality is higher in females compared to males in this watershed (e.g., Roscoe et al. 2011; Burnett et al. 2014). Numerous field studies have demonstrated that exposure to elevated temperatures is associated with increased mortality (Naughton et al 2005; Crossin et al 2008; Martins et al 2012; Burnett et al 2014), possibly due to reduced aerobic and cardiac scopes, and higher EPOC (Lee et al. 2003; Farrell et al. 2008; Eliason et al. 2013). Here, dam passage was directly impaired if water temperatures exceeded T_{opt} for aerobic scope. Moving forward, fishways and attraction flows should be designed and operated in

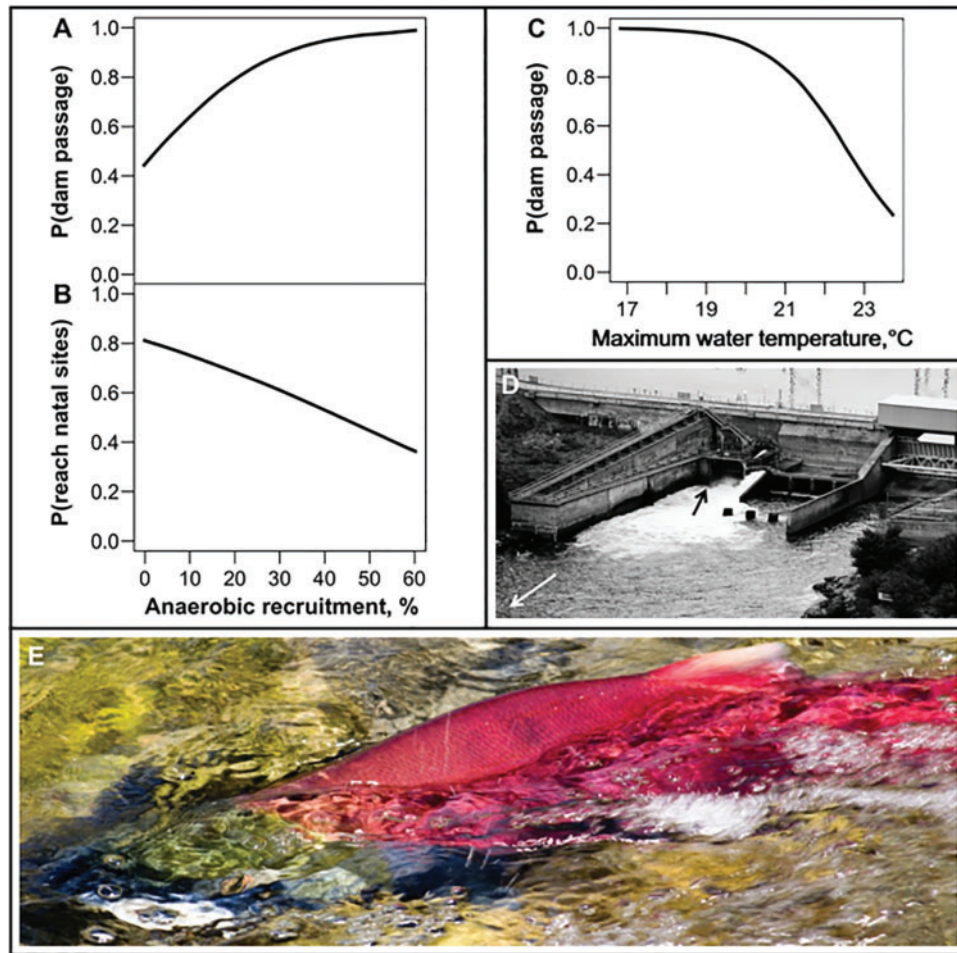


Fig. 4 Predicted probability of Gates Creek sockeye salmon (*Oncorhynchus nerka*) passing Seton Dam (A) and reaching natal spawning grounds (B) in relation to the extent of anaerobic swimming through fishway attraction flows. (C) Depiction of the predicted probability of sockeye salmon passing Seton Dam in relation to the maximum water temperature successful and unsuccessful fish experienced directly below the dam. (D) Seton Dam and the release of attraction flows adjacent to the fishway entrance (black arrow). White arrow indicates flow direction. (E) Spawning Gates Creek sockeye salmon. Photographer: Nicholas Burnett.

a manner that minimizes exposure to supraoptimal water temperatures and flows, in order to maximize successful dam passage and survival to spawning habitats.

Case Study 3: Smallmouth bass parental care

The level of locomotor activity undertaken by wild fish varies widely among individuals, even within a species or population. Some individuals are simply more mobile than others, potentially a component of a behavioral syndrome (Conrad et al. 2011). Many organisms also exhibit diel patterns of enhanced locomotor activity, often entrained rhythms related to feeding (e.g., Reeb 2002), and over longer time scales (e.g., months to life-times), specific life history phases, or events (e.g., migration, reproduction). This is particularly the case for fish that engage in

parental care such as the centrachid smallmouth bass (*Micropterus dolomieu*). Male smallmouth bass build a nest and court females (see Brewer and Orth 2015 for complete description of reproductive biology). Once eggs are deposited and fertilized, the female departs leaving the male to provide extended sole paternal care. During the early phases of parental care, the male must fan the nest to keep the eggs and newly hatched larvae oxygenated and free of silt while fending off potential brood predators. As the brood hatches and begins to range more widely (within a few meters of the nest), the male continues to guard the offspring until they have developed their own anti-predator tactics. The entire parental care period for smallmouth bass tends to last 2–5 weeks, depending largely on thermal conditions (hatching and offspring development is faster at warmer temperatures; Cooke et al. 2006). If the male abandons the brood prematurely, the brood

will not survive, due to either predation or lack of oxygenation from loss of fanning (reviewed in Brewer and Orth 2015).

For male smallmouth bass, nest guarding represents a major energetic challenge. The males are active 24 h a day, chasing potential nest predators (i.e., burst swimming), fanning (i.e., continual aerobic activity), and patrolling the vicinity of the nest (Hinch and Collins 1991; Cooke et al. 2002). Electromyogram telemetry studies showed that male smallmouth bass swam the equivalent of ~45–60 km per day (actual level varied across the parental care period; Fig. 5), and yet fish would rarely leave an area ~3 m from the nest site (Cooke et al. 2002). When compared to smallmouth bass living in a different lentic system outside of the parental care period (i.e., Cooke et al. 2001), the level of exercise undertaken during parental care is even more impressive (Fig. 5); activity levels were about twice as high during the parental care period for nesting males than during other periods (Cooke et al. 2002). Beyond the energetic challenges associated with engaging in exercise for extended time periods, the costs to the fish are further accentuated by the fact that the parental males reduce food consumption and are limited to opportunistic foraging on prey items in and around the nest (Hinch and Collins 1991). Because bass spawn in shallow waters, make conspicuous nests, and provide extended sole parental care, they make a good model for exploring elements of exercise physiology of wild fish with direct links to fitness.

Several physiological and ecological factors influence the behavior, energetics, and ultimately nesting success of parental male smallmouth bass. Research has revealed that circulating levels of the appetite hormone ghrelin are reduced during parental care, especially during the early stages, which coincides with the least amount of offspring independence and the most active parental care requirements from the male (Hanson et al. 2009a). Functionally, cessation of foraging during parental care is likely a protective mechanism given that redirecting metabolic resources to digestion impedes locomotor performance (Thorarensen et al., 1993; Alsop and Wood, 1997; Farrell et al., 2001) during a period when high levels of sustained activity coupled with frequent burst swimming are needed to successfully defend the brood. When male bass were fed to satiation during parental care, they exhibited decreases in burst swimming ability and aggressive behaviors towards brood predators when compared to unfed fish (Hanson et al. 2009b). Similarly, Algera et al. (unpublished data) found that experimentally

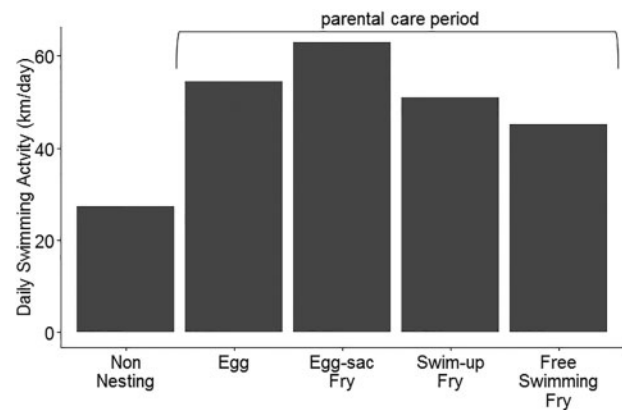


Fig. 5 Adult smallmouth bass (*Micropterus dolomieu*) swimming activity during the non-nesting period (Cooke et al. 2001) and across four stages of offspring development during parental care (Cooke et al. 2002). Data were generated using electromyogram activity transmitters.

elevated cortisol levels (primary stress hormone in fish; Barton 2002) in male smallmouth bass resulted in reduced nest guarding capabilities, including reduced activity levels as well as routine and burst swimming frequency, which are necessary for patrolling the nest (Fig. 6).

A number of studies have examined physiological and metabolic aspects of parental care in an attempt to understand correlates of parental care activity (e.g., aggression of parent, vigilance) and reproductive success (e.g., successfully raising a brood to independence). One of the most fascinating outcomes of that work has been failure to identify such relationships despite several fold differences in level of aggression. Hanson et al. (2009b) noted that neither commonly measured endocrine factors related to aggression (testosterone) nor biochemical indicators of stress (cortisol) were predictive of male aggression when standardizing by brood size. Gravel et al. (2010) examined the influence of natural variation in nest predation pressure on the aerobic and anaerobic capacities in axial white muscle and pectoral red muscle of parental smallmouth bass, but found no evidence for higher metabolic capacities in fish from lakes with increased brood predation pressure. This may be in part because of the overwhelming role of body size in reproductive success in bass. Larger parental males tend to secure the largest number of eggs from females representing higher potential fitness (Philipp et al. 1997; Suski and Philipp 2004; Barbosa and Magurran 2006), which then feeds back to further increase their parental investment as measured by vigilance and aggression towards potential nest predators and decreased likelihood of brood abandonment (Mackereth et al. 1998). To explore this issue further, Hanson and Cooke (2009)

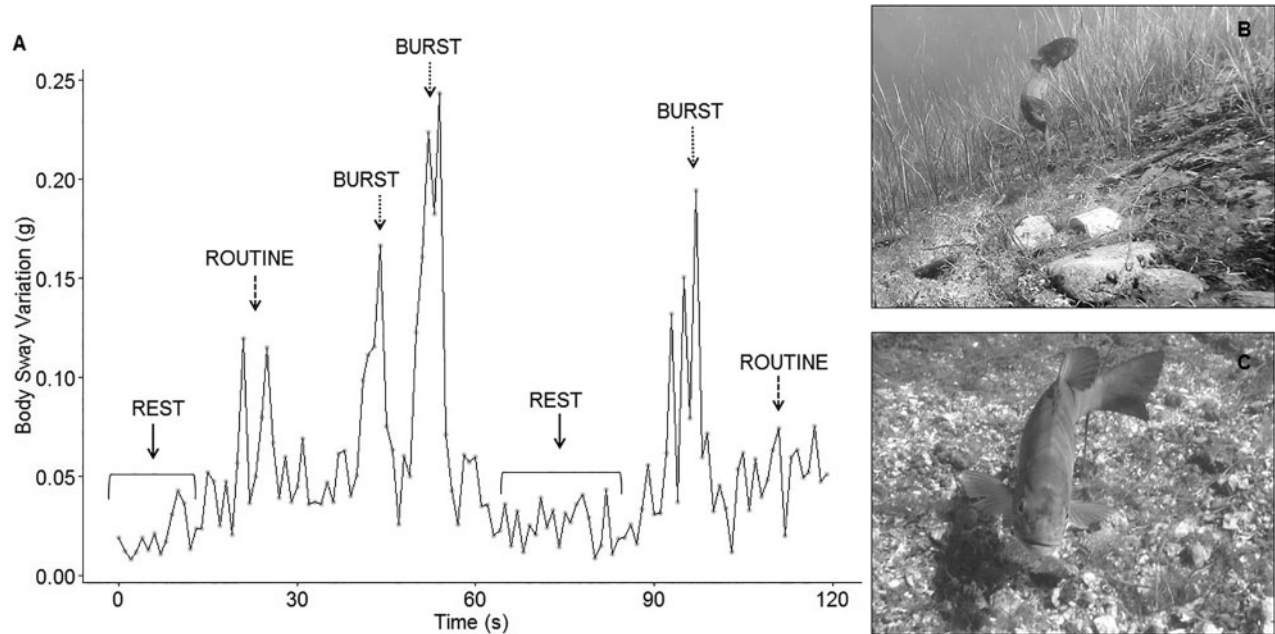


Fig. 6 (A) Example of parental care swimming behaviors of smallmouth bass (*Micropterus dolomieu*) quantified using externally attached tri-axial accelerometer biologgers. (B) A male smallmouth bass defending the nest from a brood predator (burst swimming), and (C) patrolling the nest area (routine swimming). Photo credit: M. Lawrence and T. Prystay, respectively.

studied nutritional, morphological, and physiological aspects of mate choice as inferred from brood size given that females chose which males receive eggs. This study revealed that male total length and body stoutness were the only significant predictors of female mate choice, supporting earlier studies that posited that females select larger males with higher energy levels that are able to provide parental care for longer durations (Mackereth et al. 1998). Clearly, body size and brood size matter for parental care of smallmouth bass.

It is difficult to tease apart cause and effect with this system. A small fish with a large brood is less likely to succeed than a large fish with a small brood, emphasizing that body size or some physiological correlate is probably a more ultimate driver of quality of care and reproductive success. Small fish are also younger and may lack the experience to know how to properly engage predators and also experience higher costs in that they have proportionally fewer energetic resources available and higher mass-specific metabolic rates (Wiegmann and Baylis 1995; Mackereth et al. 1998). Indeed, parental investment theory posits that animals must make trade-offs between the value of their current brood and their potential lifetime fitness (Trivers 1972; Sargent and Gross 1986). Overwinter mortality is common in centrarchids (Suski and Ridgway 2009) and is thought to be driven by energy density and body size (Cargnelli and Gross 1997). If a small parental

male with low energy reserves invests in parental care early in its life, it is possible that the current brood may succeed while the survival of the parent may be compromised by energy loss, precluding any future reproductive success. Understanding how exercise capacity intersects with life-history theory represents a fascinating avenue for future research.

Discussion

Here, we explored how environmental and physiological factors influence wild fish behavior and exercise during fitness-related activities through three case studies including bonefish foraging, Pacific salmon migration, and smallmouth bass parental care. These studies on diverse fish species spanning freshwater and marine realms highlight how environmental factors such as water temperature and flow influence fish behavior through physiological mechanisms (e.g., aerobic scope and energy expenditure) in various ecological scenarios.

Exercise is fueled primarily by aerobic respiration, and hence, the capacity to deliver oxygen to tissues is a major limiting factor in exercise capacity in fish (Pörtner and Farrell 2008; Pörtner and Lannig 2009). Because fish are ectothermic, aerobic scope is influenced heavily by water temperature (Fry 1947; Farrell et al. 2008). The role of water temperature in fish exercise is highlighted in the Bonefish foraging and Pacific salmon migration case studies. In Pacific

salmon, water temperature influences the degree of anaerobic exercise when passing challenging water flows at dams, which determines whether individuals survive to reach spawning habitats (Burnett et al. 2014). Hence, the timing of dam passage in relation to water temperature is a key determinant of biological fitness. Similarly, bonefish in Puerto Rico timed their foraging movements on nearshore flats when water temperature was near optimal for aerobic scope, which is required for exercise related to foraging (Brownscombe et al. 2017). On a broader ecological scale, in Pacific salmon aerobic scope varies between populations, and is finely tuned to migration difficulty and the distinct thermal regimes of their specific spawning tributaries (Eliason et al. 2011). These are clear examples of where aerobic scope is highly relevant to fitness enhancing activities, with complex interactions between water temperature, fish behavior, and physiology.

Animals must have the physiological capacity (i.e., cardiovascular systems, energy stores) to maintain a level of exercise required for the ecological challenges they are faced with, whether it be swimming 20–40 km/day, while migrating upriver (Pacific salmon) or swimming 40+ km/day within a restricted area as part of nest defence (smallmouth bass). In this sense, past activity levels or “training” should serve to increase their capacity to exercise (Halsey 2016). However, because energy is limited, high activity levels can also be unnecessarily high and at the expense of energy stores required for growth and reproduction (Rennie et al. 2005). Indeed, optimal acquisition (Pyke 1984) and allocation of resources (Brown et al. 2004) are considered critical for high lifetime fitness. In the Pacific salmon migration case study, we highlight examples where aerobic scope is an important determinant of Pacific salmon migration success; however, these fish also rely entirely on endogenous energy stores during migration, and often deplete 75–95% of body fat (Macdonald et al. 2000). Macdonald et al. (2000) identified the heightened energetic costs of migration due to unusually high water flows and temperatures as the likely cause of high rates of migration failure in 1997 in Fraser River sockeye salmon populations. Therefore, Pacific salmon migration success may be constrained by both exercise capacity and energy expenditure depending on the challenges they are faced with. Similarly, in the Smallmouth bass parental care example, male smallmouth bass sustain high activity levels while consuming little to no food for 2–5 weeks (Cooke et al. 2006). Hence, larger males with greater energy stores tend to be most successful at raising offspring to independence (Philipp et al. 1997;

Suski and Philipp 2004; Barbosa and Magurran 2006). Further, Gravel et al. (2010) found no correlation between exercise capacity and brood predation pressure, which would presumably increase exercise requirements to successfully defend the offspring. It is possible that aerobic scope is not as important to nesting smallmouth bass as the amount and efficient use of energy stores, but further research is needed to determine whether aerobic scope and exercise capacity are constraining factors in smallmouth bass nesting success. It is well documented that energy reserves are a key determinant of reproductive success for diverse animal species because of the high energetic demands of offspring production and care (Drent and Daan 1980; Sandberg and Moore 1996). Moreover, there are many contexts where animals must use energy reserves judiciously because fatigue limits fitness gains (e.g., foraging; Ydenberg and Clark 1989, or predation risk; Wirsing et al. 2002; Guinet et al. 2007) across heterogeneous ecological and environmental landscapes (Gallagher et al. 2017).

In the context of climate change, there is concern that increasing water temperatures will result in reduced aerobic capacities in fishes leading to population declines (Clark et al. 2013). However, in some cases aerobic scope may not be as important of a performance metric for the subsistence of a species as others such as reproductive output (Nilsson and Lefevre 2016; Lefevre 2016). Surprisingly, despite the recognized importance of efficient energy use in various ecological contexts (e.g., Shepard et al. 2013; Pyke 1984; Wirsing et al. 2002; Guinet et al. 2007), it is rarely considered in the context of climate change (but see Tomlinson et al. 2014). Based on our case studies, we suggest there are likely certain ecological contexts where aerobic scope is highly relevant to achieving fitness activities, while in others energy conservation is more relevant. The influence of increasing water temperatures on daily energy expenditure and net energy gain may have significant impacts on some fish species in the climate change context.

Exercise is a fundamental aspect of animal ecology, as it is influenced by both extrinsic (e.g., temperature) and intrinsic (e.g., body condition) factors, and highly relevant to biological fitness. Here we explored the role of exercise in activities directly related to fitness in diverse wild fishes—foraging in coastal marine bonefish, reproductive migrations in Pacific salmon, and nest guarding in male smallmouth bass. These case studies highlight some novel approaches to studying fish exercise and metabolism in the wild using biologging and biotelemetry

platforms (see Cooke et al. 2016 for more discussion on this). Environmental factors such as temperature are clearly important drivers of the capacity for exercise in fish, which in turn influences their behavior, physiology, and fitness. While scope for activity (aerobic scope) is important in many of these contexts, conservation of energy stores is also highly relevant in many scenarios. By continuing to explore these relationships, we will gain a more mechanistic understanding on the influence of environmental factors on animal distributions, population dynamics, and individual characteristics.

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References

- Alexander EC. 1961. A contribution to the life history, biology and geographical distribution of bonefish, *Albula vulpes* (Linnaeus). Copenhagen: Carlsberg Foundation.
- Alsop D, Wood C. 1997. The interactive effects of feeding and exercise on oxygen consumption, swimming performance and protein usage in juvenile rainbow trout (*Oncorhynchus mykiss*). *J Exp Biol* 200:2337–46.
- Arnold SJ. 1983. Morphology, performance and fitness. *Am Zool* 23:347–61.
- Barbosa M, Magurran AE. 2006. Female mating decisions: maximizing fitness? *J Fish Biol* 68:1636–61.
- Barton BA. 2002. Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. *Integr Comp Biol* 42:517–25.
- Bishop CM. 1999. The maximum oxygen consumption and aerobic scope of birds and mammals: getting to the heart of the matter. *Proc R Soc Lond B Biol Sci* 266:2275–81.
- Brewer SK, Orth DJ. 2015. Smallmouth Bass *Micropterus dolomieu* Lacepède, 1802. *Am Fish Soc Symp* 82:9–26.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–89.
- Brownscombe JW, Cooke SJ, Danylchuk AJ. 2017. Spatiotemporal drivers of energy expenditure in a coastal marine fish. *Oecologia* published online (doi:10.1007/s00442-016-3800-5).
- Cargnelli LM, Gross MR. 1997. Fish energetics: larger individuals emerge from winter in better condition. *Trans Am Fish Soc* 126:153–6.
- Burnett NJ, Hinch SG, Braun DC, Casselman MT, Middleton CT, Wilson SM, Cooke SJ. 2014. Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult sockeye salmon. *Physiol Biochem Zool* 87:587–98.
- Caudill CC, Daigle WR, Keefer ML, Boggs CT, Jepson MA, Burke BJ, Zabel RW, Bjornn TC, Peery CA. 2007. Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? *Can J Fish Aquat Sci* 64:979–95.
- Clark TD, Sandblom E, Jutfelt F. 2013. Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. *J Exp Biol* 216:2771–82.
- Clutton-Brock TH. 1991. The evolution of parental care. Chichester, West Sussex: Princeton University Press.
- Colton DE, Alevizon WS. 1983. Feeding ecology of bonefish in Bahamian waters. *Trans Am Fish Soc* 112:178–84.
- Conrad JL, Weinersmith KL, Brodin T, Saltz JB, Sih A. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *J Fish Biol* 78:395–435.
- Cooke SJ, Bunt CM, Schreer JF, Wahl DH. 2001. Comparison of several techniques for mobility and activity estimates of smallmouth bass in lentic environment. *J Fish Biol* 58:573–87.
- Cooke SJ, Philipp DP, Wahl DH, Weatherhead PJ. 2006. Parental care energetics of six syntopic centrarchid fishes. *Oecologia* 148:235–49.
- Cooke SJ, Philipp DP, Weatherhead PJ. 2002. Parental care patterns and energetics of smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*) monitored with activity transmitters. *Can J Zool* 80:756–70.
- Cooke SJ, Brownscombe JW, Raby GD, Broell F, Hinch SG, Clark TD, Semmens JM. 2016. Remote bioenergetics measurements in wild fish: opportunities and challenges. *Comp Biochem Physiol A Physiol* 202:23–37.
- Crabtree RE, Stevens C, Snodgrass D, Stengard FJ. 1998. Feeding habits of bonefish, *Albula vulpes*, from the waters of the Florida Keys. *Fish Bull* 96:754–66.
- Crossin GT, Hinch SG, Farrell AG, Higgs DA, Lotto AG, Oakes JD, Healey MC. 2004. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *J Fish Biol* 65:788–810.
- Crossin GT, Hinch SG, Cooke SJ, Welch DW, Patterson DA, Jones SRM, Lotto AG, Leggatt RA, Mathes MT, Shrimpton JM, et al. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. *Can J Zool* 86:127–40.

- Drent R, Daan S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–52.
- Eliason EJ, Clark TD, Hague MJ, Hanson LM, Gallagher ZS, Jeffries KM, Gale MK, Patterson DA, Hinch SG, Farrell AP. 2011. Differences in thermal tolerance among sockeye salmon populations. *Science* 332:109–12.
- Eliason EJ, Wilson SM, Farrell AP, Cooke SJ, Hinch SG. 2013. Low cardiac and aerobic scope in a coastal population of sockeye salmon *Oncorhynchus nerka* with a short upriver migration. *J Fish Biol* 82:2104–12.
- Farrell AP, Gallagher PE, Routledge R. 2001. Rapid recovery of exhausted adult coho salmon after commercial capture by troll fishing. *Can J Fish Aquat Sci* 58:2319–24.
- Farrell AP, Hinch SG, Cooke SJ, Patterson DA, Crossin GT, Lapointe M, Mathes MT. 2008. Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiol Biochem Zool* 81:697–709.
- Fry FEJ. 1971. The effect of environmental factors on the physiology of fish. *Fish Physiol* 6:1–98.
- Gallagher AJ, Creel S, Wilson RJ, Cooke SJ. 2017. Energy landscapes and the landscape of fear. *Trends Ecol Evol* published online (doi:10.1016/j.tree.2016.10.010).
- Gallaugh PE, Thorarensen H, Kiessling A, Farrell AP. 2001. Effects of high intensity exercise training on cardiovascular function, oxygen uptake, internal oxygen transfer and osmotic balance in chinook salmon (*Oncorhynchus tshawytscha*) during critical speed swimming. *J Exp Biol* 204:2861–72.
- Gannon R, Taylor MD, Suthers IM, Gray CA, van der Meulen DE, Smith JA, Payne NL. 2014. Thermal limitation of performance and biogeography in a free-ranging ectotherm: insights from accelerometry. *J Exp Biol* 217:3033–7.
- Gravel M-A, Couture P, Cooke SJ. 2010. Brood predation pressure during parental care does not influence parental enzyme activities related to swimming activity in a teleost fish. *Comp Biochem Physiol A Physiol* 155:100–6.
- Groot C, Margolis L. 1991. Pacific salmon life histories. Vancouver, Canada: UBC press.
- Guinet C, Domenici P, De Stephanis R, Barrett-Lennard L, Ford JKB, Verborgh P. 2007. Killer whale predation on bluefin tuna: exploring the hypothesis of the endurance-exhaustion technique. *Mar Ecol Prog Ser* 347:111–9.
- Halsey LG. 2016. Do animals exercise to keep fit? *J Anim Ecol* published online (doi: 10.1111/1365-2656.12488).
- Hanson KC, Cooke SJ. 2009. Nutritional condition and physiology of paternal care in two congeneric species of black bass (*Micropterus* spp.) relative to stage of offspring development. *J Comp Physiol B* 179:253–66.
- Hanson KC, O'Connor CM, Van Der Kraak G, Cooke SJ. 2009a. The relative roles of parental investment and organismal condition in parental aggression in smallmouth bass. *Horm Behav* 55:495–9.
- Hanson KC, Abizaid A, Cooke SJ. 2009b. Causes and consequences of voluntary anorexia during the parental care period of wild male smallmouth bass (*Micropterus dolomieu*). *Horm Behav* 56:503–9.
- Hinch SG, Bratty J. 2000. Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. *Trans Am Fish Soc* 129:598–60.
- Hinch SG, Collins NC. 1991. Importance of diurnal and nocturnal nest defense in the energy budget of male smallmouth bass: insights from direct video observations. *Trans Am Fish Soc* 120:657–63.
- Hinch SG, Rand PS. 2000. Optimal swimming speeds and forward-assisted propulsion: energy-conserving behaviours of upriver-migrating adult salmon. *Can J Fish Aquat Sci* 57:2470–8.
- Huey RB, Hertz PE. 1984. Is a jack-of-all temperatures a master of none? *Evolution* 38:441–4.
- Humston R, Ault JS, Larkin MF, Luo J. 2005. Movements and site fidelity of the bonefish *Albula vulpes* in the northern Florida Keys determined by acoustic telemetry. *Mar Ecol Prog Ser* 291:237–48.
- Kleiber M. 1975. The fire of life: An introduction to animal energetics. 2nd edn. Huntington: RE Krieger Pub Co.
- Le Galliard JF, Clobert J, Ferrière R. 2004. Physical performance and Darwinian fitness in lizards. *Nature* 432:502–5.
- Lee CG, Farrell AP, Lotto A, MacNutt MJ, Hinch SG, Healey MC. 2003. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *J Exp Biol* 206:3239–51.
- Lefevre S. 2016. Are global warming and ocean acidification conspiring against marine ectotherms? A meta-analysis of the respiratory effects of elevated temperature, high CO₂, and their interaction. *Conserv Physiol* 4: cow009.
- Lind J, Cresswell W. 2005. Determining the fitness consequences of antipredation behavior. *Behav Ecol* 16:945–56.
- Macdonald JS, Canada. Dept. of Fisheries and Oceans. Pacific Region. Science Branch. 2000. *Mortality during the migration of Fraser River sockeye salmon (Oncorhynchus nerka): a study of the effect of ocean and river environmental conditions in 1997*. Burnaby, BC: Fisheries and Oceans Canada, Science.
- Mackereth RW, Noakes DL, Ridgway MS. 1998. Size-based variation in somatic energy reserves and parental expenditure by male smallmouth bass, *Micropterus dolomieu*. *Environ Biol Fish* 56:263–75.
- Marden JH, Rollins RA. 1994. Assessment of energy reserves by damselflies engaged in aerial contests for mating territories. *Anim Behav* 48:1023–30.
- Martins EG, Hinch SG, Patterson DA, Hague MJ, Cooke SJ, Miller KM, Robichaud D, English KK, Farrell AP. 2012. High river temperature reduces survival of sockeye salmon (*Oncorhynchus nerka*) approaching spawning grounds and exacerbates female mortality. *Can J Fish Aquat Sci* 69:330–42.
- Milinski M, Heller R. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* 275:642–4.
- Milner-Gulland EJ, Fryxell JM, Sinclair AR. 2011. Animal migration: a synthesis. New York (NY): Oxford University Press.
- Muñoz NJ, Farrell AP, Heath JW, Neff BD. 2015. Adaptive potential of a Pacific salmon challenged by climate change. *Nat Clim Chang* 5:163–6.
- Murchie KJ, Cooke SJ, Danylchuk AJ, Danylchuk SE, Goldberg TL, Suski CD, Philipp DP. 2013. Movement patterns of bonefish (*Albula vulpes*) in tidal creeks and coastal waters of Eleuthera, The Bahamas. *Fish Res* 147:404–12.
- Nadeau PS, Hinch SG, Hruska KA, Pon LB, Patterson DA. 2010. The effects of experimental energy depletion on the

- physiological condition and survival of adult sockeye salmon (*Oncorhynchus nerka*) during spawning migration. *Environ Biol Fish* 88:241–51.
- Naughton GP, Caudill CC, Keefer ML, Bjornn TC, Stuehrenberg LC, Peery CA. 2005. Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Can J Fish Aquat Sci* 62:30–47.
- Nilsson GE, Crawley N, Lunde IG, Munday PL. 2009. Elevated temperature reduces the respiratory scope of coral reef fishes. *Glob Chang Biol* 15:1405–12.
- Nilsson GE, Lefevre S. 2016. Physiological challenges to fishes in a warmer and acidified future. *Physiology* 31:409–17.
- Nowell LB, Brownscombe JW, Gutowsky LFG, Murchie KJ, Suski CD, Danylchuk AJ, Shultz A, Cooke SJ. 2015. Swimming energetics and thermal ecology of adult bonefish (*Albula vulpes*): A combined laboratory and field study in Eleuthera, The Bahamas. *Environ Biol Fish* 98:2133–46.
- O'Connor CM, Norris DR, Crossin GT, Cooke SJ. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere* 5: art28. doi: 10.1890/ES13-00388.1.
- Philipp DP, Toline CA, Kubacki MF, Philipp DB, Phelan FJ. 1997. The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. *N Am J Fish Manag* 17:557–67.
- Pon LB, Hinch SG, Cooke SJ, Patterson DA, Farrell AP. 2009. Physiological, energetic and behavioural correlates of successful fishway passage of adult sockeye salmon *Oncorhynchus nerka* in the Seton River, British Columbia. *J Fish Biol* 74:1323–36.
- Pörtner HO, Farrell AP. 2008. Physiology and climate change. *Science* 322:690–2.
- Pörtner HO, Lannig G. 2009. Oxygen and capacity limited thermal tolerance. *Fish Physiol* 27:143–91.
- Priede IG. 1977. Natural selection for energetic efficiency and the relationship between activity level and mortality. *Nature* 267:610–1.
- Pyke GH. 1984. Optimal foraging theory: a critical review. *Annu Rev Ecol Syst* 15:523–75.
- Rand PS, Hinch SG, Morrison J, Foreman MGG, MacNutt MJ, Macdonald JS, Healey MC, Farrell AP, Higgs DA. 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. *Trans Am Fish Soc* 135:655–67.
- Reeb SG. 2002. Plasticity of diel and circadian activity rhythms in fishes. *Rev Fish Biol Fish* 12:349–71.
- Rennie MD, Collins NC, Shuter BJ, Rajotte JW, Couture P. 2005. A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower. *Can J Fish Aquat Sci* 62:767–80.
- Robson MA, Miles DB. 2000. The association between social dominance and physiological performance in a lizard. *Funct Ecol* 14:338.
- Roscoe DW, Hinch SG, Cooke SJ, Patterson DA. 2011. Fishway passage and post-passage mortality of up-river migrating sockeye salmon in the Seton River, British Columbia. *River Res App* 27:693–705.
- Sandberg R, Moore FR. 1996. Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. *Oikos* 77:577–81.
- Sargent RC, Gross MR. 1986. Williams' principle: an explanation of parental care in teleost fishes. In: Pitcher TJ (editor). *The behaviour of teleost fishes*. Beckenham, UK: Croom Helm Ltd.
- Scarabello M, Heigenhauser GJ, Wood CM. 1992. Gas exchange, metabolite status and excess post-exercise oxygen consumption after repetitive bouts of exhaustive exercise in juvenile rainbow trout. *J Exp Biol* 167:155–69.
- Shepard EL, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB. 2013. Energy landscapes shape animal movement ecology. *Am Nat* 182:298–312.
- Smith C, Wootton RJ. 1995. The costs of parental care in teleost fishes. *Rev Fish Biol Fish* 5:7–22.
- Steinhausen MF, Sandblom E, Eliason EJ, Verhille C, Farrell AP. 2008. The effect of acute temperature increases on the cardiorespiratory performance of resting and swimming sockeye salmon (*Oncorhynchus nerka*). *J Exp Biol* 211:3915–26.
- Suski CD, Philipp DP. 2004. Factors affecting the vulnerability to angling of nesting male largemouth and smallmouth bass. *Trans Am Fish Soc* 133:1100–6.
- Suski CD, Ridgway MS. 2009. Winter biology of centrarchid fishes. In: Cooke SJ, Philipp DP, editors. *Centrarchid fishes: diversity, biology, and conservation*. West Sussex, UK: Wiley-Blackwell. p. 264–92.
- Tewksbury JJ, Huey RB, Deutsch CA. 2008. Putting the heat on tropical animals. *Science* 320:1296–7.
- Thorarensen H, Gallagher PE, Kiessling AK, Farrell AP. 1993. Intestinal blood flow in swimming chinook salmon *Oncorhynchus tshawytscha* and the effects of haematocrit on blood flow distribution. *J Exp Biol* 179:115–29.
- Tytler P, Calow P. 1985. *Fish energetics: new perspectives*. Australia: Croom Helm Ltd.
- Tomlinson S, Arnall SG, Munn A, Bradshaw SD, Maloney SK, Dixon KW, Didham RK. 2014. Applications and implications of ecological energetics. *Trends Ecol Evol* 29:280–90.
- Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. *Sexual selection and the descent of man*. Chicago: Aldine. p. 136–79.
- Wallace EM. 2014. *Assessing biodiversity, evolution, and biogeography in bonefishes (Albuliformes): resolving relationships and aiding management*. PhD Thesis, University of Minnesota.
- Wiegmann DD, Baylis JR. 1995. Male body size and paternal behaviour in smallmouth bass, *Micropterus dolomieu* (Pisces: Centrarchidae). *Anim Behav* 50:1543–55.
- Wirsing AJ, Steury TD, Murray DL. 2002. Relationship between body condition and vulnerability to predation in red squirrels and snowshoe hares. *J Mammal* 83:707–15.
- Wood CM, Turner JD, Graham MS. 1983. Why do fish die after severe exercise? *J Fish Biol* 22:189–201.
- Ydenberg RC, Clark CW. 1989. Aerobiosis and Anaerobiosis during diving by western grebes: an optimal foraging approach. *J Theory Biol* 139:437–49.