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Tony Farrell

Animals either adapt to adversity over an evolutionary time scale or die out. Adult sockeye salmon that make an upstream spawning migration in the Fraser River watershed in British Columbia, Canada are a remarkable example of this because some populations must make a far more arduous swim to reach their natal spawning area than others. Moreover, sockeye spawn only once in their lifetime, and so the success (or failure) of their spawning migration plays a huge role in determining their lifetime fitness. Consequently, there may be lessons to be learnt about fish passage by studying the performance characteristics that have evolved in salmonids such as sockeye salmon. If so, the implication then is that fish have already evolved the means to by-pass manmade barriers, provided the construction of the fish passageway properly recognizes what fish can and cannot do. Minimally, by understanding the rules that set the swimming capabilities and capacities of fishes, we can adjust existing barriers to improve fish passage. Moreover, and given the inevitability of a warmer future for aquatic environments, if we can understand how temperature modulates these capacities and capabilities, we can make logical predictions about what this might portend for fish passage. In the following, I will advance some rules and illustrate how local adaptation to different hydraulic and thermal challenges currently exists among sockeye salmon populations within a single watershed. Thus, we have to look beyond species differences in fish passage capabilities to significant intraspecific differences as well as significant differences between sexes.

Before advancing six important rules to consider for fish passage, it is important to appreciate the watershed where I have spent decades studying the amazing migratory physiology of sockeye salmon and their cardiorespiratory life-support system. Sockeye salmon populations in the Fraser River are an exquisite model watershed for a variety of reasons. Foremost, sockeye salmon still migrate in huge numbers: many millions in most years. Second, the difference in the distance they migration upstream is huge: as little as a 100 km but as much as 1000 km before reaching their natal spawning area. Third, all of their river migration is performed without feeding over several weeks; they have laid down sufficient lipid stores ahead of time to fuel this migration without knowing exactly what environmental conditions they will encounter. Fourth, the remarkable fidelity to a natal spawning area means that individual DNA-typing in conjunction with implantation of thermal logging and biotracking devices during early river migration means that we know which part of the watershed they will end up in if their migration has been successful (COOKE et al. 2008, FARRELL et al. 2008). Lastly, while rules for fish passage certainly exist, it is also evident that sockeye salmon appear to have evolved variable strategies to deal with hydraulic and temperature

challenges during upstream migration – these are challenges that individuals have never previously experienced, but are likely challenges that have been subjected to natural selection over an evolutionary timescale. Yet, there are clear limits to those strategies, especially because river temperatures are warming in this era of global climate change. For this reason alone, it is vital to consider the influence of temperature on the fish cardiorespiratory performance when examining the rules and strategies for fish passage.

The six foundational rules that I think are of fundamental importance in any consideration of fish passage are founded on the cardiorespiratory system – a critical life support system. The cardiorespiratory system is reasonably well understood in fishes and even better understood in humans. However, these rules are to be used only as a general guide because what an individual fish can and cannot do within a given environmental setting is set out by its individual morphological, physiological and biochemical capabilities, as dictated by its genetics. In terms of genetics, capabilities importantly differ among species, among certain populations of a species and even between sexes, as shown by the examples below. It is for this very reason that a case will be made for locally derived criteria that take full account of the possibility for intraspecific variability in physiological capacities, as well as flexibility in strategies.

Rule 1: Temperature determines a fish's minimum oxygen needs for survival.

Simple thermodynamics dictate that the myriad of biochemical reactions necessary for life increase exponentially with temperature (within limits, that is). Fish are typically at the same temperature as the surrounding water and this means that a fish's basic (minimum) O_2 requirement (and food) needed to maintain itself must approximately double with every 10 $^{\circ}$C increase in water temperature (FRY 1947, 1971; FRY & HART 1948). This minimum O_2 requirement is termed standard metabolic rate (SMR) in fishes, and it increases exponentially with temperature up to the thermal tolerance limits of a fish, which differs among fish species and populations. The intrinsic heart rate of fishes similarly increases with temperature, but peaks and may also become arrhythmic before a fish succumbs to extreme warming (CASSELMAN et al. 2012, ELIASON et al. 2013b).

Of course, there must be sufficient O_2 in the water to support SMR, otherwise life becomes time-limited. If water is fully air-saturated this should not be a specific problem, despite certain fishermen's tales to the contrary (STEINHAUSEN et al. 2008, ELIASON et al. 2013b, FARRELL 2016). Fish can partially avoid this relationship with temperature if they can acclimate to a new temperature over time, but thermal acclimation has its limitations (FRY 1971, ELLIOTT 1975, ANTILLA et al. 2014).

Fishes have an exquisite ability to sense water temperature, which they use routinely to seek preferred water temperatures. Moreover, they can exploit thermal stratification and thermal gradients to their advantage to save energy. By seeking out and using cold water as a refugia, they can reduce SMR and food requirements (FARRELL et al. 2008, ELLIOT & ELLIOT 2010). Adult sockeye salmon use this flexible thermal strategy; they are known to exploit cool ground water entering the river as well as cool water at depth in lakes during their migration to natal spawning areas. Also, juvenile sockeye salmon in rearing lakes show a diurnal feeding migration, feeding in warm surface layers and digesting the meal in cooler water at depth to lower SMR.

Rule 2: Locomotion in water has large energy cost that is evident from the exponential increasing the oxygen with swimming speed.

Any activity of a fish ultimately has an O_2 cost (e. g., O_2 uptake while digesting a meal may be double SMR). In terms of fish passage, the O_2 cost of swimming increases exponentially with swimming speed as a result of the high density and viscosity of water through which they must move. However, fish have maximum metabolic rate (MMR) that cannot be exceeded when swimming for prolonged periods (minutes to hours) (FRY & HART 1948, FRY 1971, BRETT 1971). Generally, fish with a higher MMR have higher maximum prolonged swimming speed. (Note: Because fish rarely keep still SMR is difficult to estimate during SMR measurements (CHABOT et al. 2016). Consequently, routine metabolic rate (RMR) is often reported instead, which is slightly higher than SMR.)

Size and morphology matter in terms of swimming capabilities. For example, the power generated by skeletal muscle is proportional to the cross-sectional area of the muscle (check out an Olympic weightlifter), which for a salmon is the cross-section of the body near to the dorsal fin. Consequently, a large fish within a species can achieve a higher absolute swimming speed than a smaller fish. The difference in absolute swimming speed with size can be almost normalized by expressing swimming speed as a function of fish body length (BL), but relative swimming speed expressed in BL/s does decrease somewhat with size. The implication for fishway design is that, within a species, a large fish can sustain higher absolute speeds than a small fish. All the same, small fish are better suited than larger fish to use behavioural strategies to their advantage by exploiting boundary layer conditions associated with the bottom and sides of a fishway, even though small fish tend to buffeted more in turbulent conditions than large fish. Morphological adaptations associated with head and pectoral fin shape can also help fish use boundary conditions in fishways.

Rule 3: Temperature also modulates a fish's maximum capacity to supply oxygen.

The O_2 available for prolonged swimming activity is the difference between MMR and SMR, which is termed absolute aerobic scope (AAS). MMR also depends on temperature, but not in exactly the same way as SMR; MMR typically reaches its peak at a temperature below the for peak SMR (LEE et al. 2003a). Consequently, AAS typically peaks several degrees cooler than the temperature at which a fish succumbs when excessively warmed. The reaction norm of AAS with temperature is termed a Fry aerobic scope curve and comparison of these curves among fish species and populations provides great insight as to relative swimming capacity as a function of water temperature (FARRELL et al. 2008). Indeed, the vastly different Fry aerobic scope curves that exist among fish species has been common knowledge for over half a century (FRY 1947, 1971; FRY & HART 1948). The intraspecific difference in Fry aerobic scope curves among populations of adult sockeye salmon trying to reach their spawning area, however, is relatively new knowledge. Moreover, these new Fry aerobic scope curves for adult Fraser River sockeye salmon have revealed just how well tailored they are to the population-specific hydraulic and temperature challenges faced during river migration (ELIASON et al. 2011, 2013a, 2013b). Like their lipid stores (CROSSIN et al. 2004), Fry aerobic scope curves for different adult Fraser River sockeye salmon populations likely have been subjected to natural selection over an evolutionary timescale. Indeed, using biotelemetry of one natural population during a period of severely high river temperatures showed that

individual fish had a much better chance of reaching their spawning ground when they swam at the optimal temperature for AAS (FARRELL et al. 2008, MATHES et al. 2010). Consequently, knowing the Fry aerobic scope curve for a fish species will help make better predictions of fish performance in a fishway at the height of summer as well as in future river warming scenarios.

Delivering oxygen to exercising muscle requires enhanced blood flow to the skeletal muscle, which is powered by the heart. Intriguingly, the entire cardiorespiratory system of adult Fraser River sockeye salmon appears to be finely tuned at the population level to the hydraulic and temperature encountered during their quest to contribute to the next generation. Indeed, it was shown that scope for increasing heart rate and cardiac output also has the same optimal temperatures as AAS at the population level, and cardiac size is directly related to migration distance (ELIASSON et al. 2011, ELIASON et al. 2013c, ELIASON & FARRELL 2016).

Rule 4: Maximum swimming speeds involve different gaits and muscle types.

While prolonged, steady-state swimming is largely powered by red skeletal muscle, the fastest speeds of a fish are powered by white skeletal muscle. White skeletal muscle typically represents around 50 % of a fish's body mass and generates ATP predominantly via the glycolytic breakdown of glucose to lactate. Glycolytic ATP production can occur at a faster rate than ATP production via aerobic oxidative phosphorylation in mitochondria. Consequently, white skeletal muscle can contract at a faster rate, which results in a faster tailbeat frequency. Another fundamental physiological relationship concerning muscle contraction is that swimming speed and duration are inversely related. Thus, burst speeds can be maintained for no more than a few minutes to attain ground speed in a fishway. Sprint speeds are faster still but cannot be sustained for seconds; sprints would be used by a fish to negotiate the fastest hydraulic challenges of a fishway. The transition from steady-state to burst swimming is considered a gait change, much like a horse switching from a canter to a gallop (PEAKE & FARRELL 2005, 2006). This gait change can be readily seen in a fish in an aquatic treadmill when water velocity is progressively increased, e. g., labriform swimmers will stop swimming using only their pectoral fins and transition to more powerful tailbeats. With carangiform swimmers in a swim tunnel, tailbeats can become periodic at the fastest frequencies – termed burst-and-coast swimming – possibly because the fish is maintaining station within the swimming section of the treadmill rather than continuously making a steady ground speed. These bursts typically last well under a minute. If the fish is making ground speed, the new gait can be maintained for up to several minutes depending on the water velocity, or until the fish fatigues or exhausts. In contrast, prolonged, steady-state swimming in sockeye salmon can be maintained for hours (STEINHAUSEN et al. 2008).

Ultimately, glycolytic swimming activity is self-limiting due to either waste build up, which is indicated by the lactate concentration building up in the blood (JAIN & FARRELL 2003), or fuel depletion, which is indicated by a depletion of glycogen stores in skeletal white muscle tissues, or some combination. If a fish is chased for several minutes, it will not fully deplete its muscle glycogen stores provided it is in good health and well fed; it takes several bouts of such chasing to achieve glycogen depletion. In contrast, prolonged and sustained swimming for minutes to hours is fueled by oxidation of lipid stores (hence the need to increase O_2 uptake with swimming). Thus, it should not be a surprise that adult sockeye salmon populations facing a longer river migration to their natal spawning have a higher lipid content prior to river entry (CROSSIN et al. 2004).

Rule 5: Full recovery from fatigue takes hours, while fully recovery from exhaustion takes even longer.

If a fish is swum to fatigue by progressively increasing water velocity, it can resume swimming at a lower velocity. However, a fish swum to exhaustion cannot swim at all until after a period of recovery. Swimming to fatigue and exhaustion both involve glycolytic swimming, which does not have an immediate O_2 cost. Much like spending on a credit card, the cost of glycolytic swimming comes later, during recovery when O_2 uptake is elevated considerably even though the fish may not be swimming. After fatigue, the elevated O_2 uptake (i. e., above SMR) decreases exponential with recovery time and may last 1-4 h before full recovery (BRETT 1971, LEE et al. 2003b). Even so, a healthy salmonid can repeat an incremental swimming test after about a 1-h recovery period and without full recovery (JAIN et al. 1997, 1998; JAIN & FARRELL 2003. However, an exhausted full metabolic recovery (and elevated O_2 uptake) can take 10-20 h (ZHANG et al. 2018). After both fatigue and exhaustion, it is the oxygen stores and high energy phosphate stores that are restored first and within the first hour, while restoration of glycogen and lipid stores take much longer.

The length recovery periods have critical consequences for fishway designs. Perhaps, the last thing the design of a fishway should do is leave the fish fatigued or exhausted as it exits. It is then a 'lame duck' while recovering in an upstream area where avian predators will quicker learn that fish are easier to capture than usual! Preferably, the velocity profile should not exhaust a fish; if does there may needs to be a refuge area for a recovery period up to 1 h. Repeated exhaustion during a fishway passage will severely deplete glycogen stores, which would take many hours to recover. Velocity profiles that fatigue a fish will mean a recovery period of at least 30 min before swimming performance approaches its previous level. These general suggestions should be tested at the species level as relevant for a particular fishway.

Rule 6: Differences between the sexes can be important.

Sexual maturation heightens sex differences in fishes. This is particularly evident in sockeye salmon. Adult males and females are typical indistinguishable before they enter the river; they are the same size and body mass. As they mature, they take on different body shapes and different brilliant red colorations. While females invest a remarkable 14 % of their body mass into eggs, males invest a paltry 4-6 % of body mass into gametes (they have stopped feeding). Biotelemetry has revealed different swimming behaviours too. Females seem to 'conserve' energy by taking the most direct and less arduous route upstream, while males seem to expend more energy moving across the river more often (HINCH et al. 2006). Perhaps correspondingly, male sockeye salmon can increase their heart mass by up to 50 % as they sexually mature; females do not.

Of great concern for fish passage design is that numerous studies have shown post-handling mortality and failed migration success to be higher for mature female salmonids than for mature males, a sex difference that shows up when migration conditions are warmer than normal (HINCH et al. 2012). So warm temperature and sex appear to be having interactive effects. Why this is so is unclear, but special consideration clearly needs to be given to passage of mature female fish during the height of summer.

In conclusion, these six fundamental rules that are based on sound physiological principles as well as empirical data are not intended to be exhaustive. But they do set a basic framework from which fishways can be better designed, at least in principle. The selected reading below and many of the references contained above provide additional details and considerations, as well as examples of empirical data. Ultimately, the design must satisfy local environmental conditions and fish species, which have the potential to vary considerably from site to site.

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