

Aerobic swimming in intensive finfish aquaculture: applications for production, mitigation and selection

McKenzie David ^{1,*}, Palstra Arjan P. ², Planas Josep ³, Mackenzie Simon ⁴, Bégout Marie-Laure ⁵, Thorarensen Helgi ⁶, Vandeputte Marc ^{5,7}, Mes Daan ⁸, Rey Sonia ⁴, De Boeck Gudrun ⁹, Domenici Paolo ¹⁰, Skov Peter V. ¹¹

¹ MARBEC Université Montpellier CNRS IRD Ifremer Montpellier, France

² Research Animal Breeding and Genomics Wageningen Livestock Research Wageningen University Wageningen ,he Netherlands

³ Facultat de Biologia Universitat de Barcelona Barcelona ,Spain

⁴ Institute of Aquaculture University of Stirling Stirling, UK

⁵ Plateforme Experimentale de Palavas Ifremer Palavas-les-Flots, France

⁶ Hólar University College Sauðárkrókur Iceland

⁷ INRAE AgroParisTech GABI Université Paris-Saclay Jouy-en-Josas, France

⁸ Department of Production Animal Clinical Sciences Norwegian University of Life Sciences Oslo ,Norway

⁹ Systemic Physiological and Ecotoxicological Research Department of Biology University of Antwerp Antwerp ,Belgium

¹⁰ IAS-CNR Istituto per lo studio degli impatti Antropici e Sostenibilità in ambiente marino Sezione di Oristano Località Sa Mardini Torregrande (Oristano),Italy

¹¹ DTU Aqua Section for Aquaculture The North Sea Research Centre Technical University of Denmark Hirtshals ,Denmark

* Corresponding author : David McKenzie, email address : david.mckenzie@cnr.fr

Abstract :

We review knowledge on applications of sustained aerobic swimming as a tool to promote productivity and welfare of farmed fish species. There has been extensive interest in whether providing active species with a current to swim against can promote growth. The results are not conclusive but the studies have varied in species, life stage, swimming speed applied, feeding regime, stocking density and other factors. Therefore, much remains to be understood about mechanisms underlying findings of ‘swimming-enhanced growth’, in particular to demonstrate that swimming can improve feed conversion ratio and dietary protein retention under true aquaculture conditions. There has also been research into whether swimming can alleviate chronic stress, once again on a range of species and life stages. The evidence is mixed but swimming does improve recovery from acute stresses such as handling or confinement. Research into issues such as whether swimming can improve immune function and promote cognitive function is still at an early stage and should be encouraged. There is promising evidence that swimming can inhibit precocious sexual maturation in some species, so studies should be broadened to other species where precocious maturation is a problem. Swimming performance is a heritable trait and may prove a useful selection tool, especially if it is related to overall robustness. More research is required to

better understand the advantages that swimming may provide to the fish farmer, in terms of production, mitigation and selection.

Keywords : aerobic exercise, growth, maturation, selection, stress, welfare

Introduction

The aquaculture research community is interested in the potential applications of swimming exercise as a tool to promote the productivity and welfare of some intensively farmed fish species. This interest crystallized as an EU COST Action (FA1304 Fitfish) that provided a forum to discuss the potential uses of exercise in finfish aquaculture. A critical reappraisal of the literature is now timely (Palstra and Planas, 2013), so this review provides a concise analysis of current knowledge focussing on three major applications for swimming, namely production, mitigation and selection.

With regard to production, sustained aerobic exercise has been reported to stimulate growth and/or improve feed conversion for a variety of farmed species, under experimental conditions (Davison and Herbert, 2013). This is of obvious potential interest, we review the latest evidence and the potential underlying mechanisms, which range from animal behaviour (Jørgensen and Jobling, 1993; Skov et al., 2011) to muscle cell biology (Ibarz et al., 2011). In terms of mitigating the deleterious impacts of intensive aquaculture on the welfare of fishes, exercise has been reported to alleviate chronic stress (Young and Cech, 1993) and to promote recovery from acute stresses (McKenzie et al., 2012; Milligan et al., 2000). It may also improve disease resistance (Castro et al., 2011), promote neuroplasticity and cognition (Mes et al., 2020), and inhibit precocious sexual maturation (Graziano et al., 2018; Palstra et al., 2010a). We review the evidence for these positive effects and their underlying mechanisms. We briefly consider how observation of swimming behaviour may provide ‘operational welfare indicators’ (OWI), especially in early life stages.

In terms of using exercise as a tool for selection, this could have various applications. Exercise tests may be useful in identifying robust animals within a population that are best suited for grow out, for example for transfer to sea pens, and may be able to distinguish fish for their stress coping styles. Exercise tests could also be used for trans-generational selection of robust families, so we review the evidence that exercise performance is a heritable trait in fishes (Vandeputte et al., 2016).

Exercise and production: effects on growth

Studies on the effects of exercise training on growth in fishes arose initially to resolve the question of whether fish muscle displayed the same degree of plasticity as their mammalian counterparts, when subjected to an exercise regime (Davison, 1989). Several parallel fields of fundamental research examined how swimming exercise (and 'training') might affect variables

such as muscle fibre sizes and densities (Davison and Goldspink, 1977; Rasmussen et al., 2011), overall exercise performance capacity (Gallaughan et al., 2001), and the use of metabolic fuels (Alsop and Wood, 1997; Richards et al., 2002). There was also a research focus upon a more applied aspect, namely whether aerobic exercise could be used to improve growth rates when farming fish species that, in nature, have an active lifestyle. This subject has been extensively reviewed (Davison, 1997, 1989; Davison and Herbert, 2013; Jobling et al., 1993) but new approaches and species continue to accrue, demanding a consideration of current status and future directions. Although it is frequently reported that fishes submitted to moderate swimming exercise have higher growth rates than those held in still water or at low currents (e.g. Ibarz et al., 2011; Palstra et al., 2015; Shrivastava et al., 2018), other studies have found that swimming exercise has no, or even negative, effects on growth (e.g. Kiessling et al., 1994; McKenzie et al., 2012; Skov et al., 2015).

Growth and energy balance

At its most basic definition, growth is an increase in body mass due to consumption of food (Jobling, 2002). In principle, growth of fishes (Fig. 1) depends on the balance between the energy assimilated from consumed food and the amount of that energy dissipated for metabolism, the ‘costs of living’. These metabolic costs comprise (1) standard metabolic rate (SMR), the cost of basal organismal maintenance; (2) specific dynamic action (SDA), the costs of nutrient digestion, assimilation and tissue deposition, and (3) the costs of routine activities such as swimming, immune responses and reproduction. The remainder of the assimilated energy equals the theoretical net gain and ‘growth’ of the fish, although this is also influenced by the efficiency with which nutrients are converted to energy or tissue accretion (Brett, 1976; Brett and Groves, 1979; Jobling, 2002; Jobling et al., 1993).

An increased growth rate in fishes subjected to swimming exercise is commonly referred to as ‘improved’, ‘optimised’ or ‘enhanced’. It is essential, however, to distinguish whether an increased growth rate is simply due increased feed consumption, as opposed to increased retention of energy and nutrients. That is, from a perspective of the profitability and environmental impact of aquaculture, ‘exercise-enhanced growth’ is really only promising if it is associated with improved efficiency of how food energy is retained as body mass, namely an improved feed conversion ratio (FCR) and/or an improved retention of dietary protein.

Energetic costs of aerobic swimming

Aerobic swimming is muscular work so it of course has an energetic cost, which is typically measured indirectly as rates of oxygen uptake when fish are obliged to swim at set speeds in a swim-tunnel respirometer (Brett, 1964; Webb, 1998; McKenzie, 2011). Swimming speeds in fishes are commonly normalised to bodylengths s^{-1} ($BL s^{-1}$) to facilitate comparison among individuals of different sizes. This does not in fact completely compensate for size effects because maximum swim speeds in $BL s^{-1}$ decline significantly with length within and across fish species (Bainbridge, 1958; Beamish, 1978; Videler, 1993). The cost of swimming increases exponentially with increasing speed, because the drag a fish must overcome when swimming increases with the square of the velocity (Videler, 1993). There are various other factors that can contribute to the cost of swimming, for example the cost of gill ventilation, which may depend on the mode of ventilation and whether this changes with swimming speed (Steffensen, 1985). Furthermore, the increased ventilation and perfusion of the gills that is required to provide oxygen for aerobic swimming, will also result in increased ion and water movements across the respiratory epithelium, a phenomenon known as the osmo-respiratory compromise (Randall et al., 1972; Gonzalez & McDonald, 1992; Gallaughner et al., 2001). This may also contribute to an increased energy expenditure in exercising fish. The capacity of fishes to meet the costs of aerobic swimming is of course finite. The species-specific maximum capacity for aerobic swimming occurs at the maximum sustainable swimming speed (U_{ms}), which is taken to mean a speed that can be sustained for hours or even days without fatigue (Beamish, 1978; Blasco et al., 2020; Videler, 1993). The critical swimming speed (U_{crit}) has often been considered a relatively close approximation of U_{ms} in fishes (Hammer, 1995). The U_{crit} protocol involves imposing step-wise increases in speed in a swim-tunnel, until the fish fatigues. The U_{crit} exceeds U_{ms} because fishes transition from steady (sustainable) aerobic swimming to unsteady (unsustainable) anaerobic swimming prior to fatigue. A number of studies suggest that the maximum speed that can be sustained aerobically corresponds to about 60-80% U_{crit} (Burgetz et al., 1998; Lee et al., 2003; Wilson and Egginton, 1994).

Within the range of aerobic speeds that a fish can swim at, the energy expenditure per distance travelled is often referred to as the cost of transportation (COT) (Beamish, 1978; Davison and Herbert, 2013). This is, however, slightly misleading because it includes metabolic costs that are unrelated to the cost of locomotion, such as SMR and even the SDA (Fig. 1a). At low and moderate swimming velocities, the cost of locomotion may be the

smallest of these factors (Fig. 1a). In addition, a need for stability control at low speeds may also contribute to overall metabolic cost (Fitzgibbon et al., 2007). The cost of transport is often specified as to whether or not it includes SMR, being either total cost of transport (T_{COT}) or net cost of transport (N_{COT}) respectively (Ohlberger et al., 2006); the latter is sometimes also called the cost of swimming (COS, McKenzie et al., 2003). The T_{COT} typically shows a 'U-shape' against swimming speed, the elevated T_{COT} at low speeds (Fig. 1b) is primarily due to the SMR occupying a large proportion of the total metabolic rate, with the cost of swimming being low (Fig. 1a). The swimming speed at which the T_{COT} is the lowest has been defined as the optimal swimming speed (U_{opt} , Fig 1b) (Tucker, 1970; Videler, 1993). It may be important for fishes when they are foraging, where energy acquired can be proportional to the distance travelled. The U_{opt} is influenced by environmental factors such as water temperature (Claireaux et al., 2006) as well as by inherent characters of the fish, such as morphology, body size, nutritional and reproductive status (Cai et al., 2014; Kaufmann, 1990; Pettersson and Hedenström, 2000). In addition, schooling also reduces the cost of swimming (Marras et al., 2015). There are reports that spontaneous preferred swimming speed of various species coincides with their U_{opt} (e.g. Tudorache et al., 2011; Weihs et al., 1981). For farmed fishes, food is supplied in abundance and access to feed is not directly proportional to the distance covered. Thus, it could be argued that in an aquaculture context, any energy that is allocated to aerobic swimming does not promote food acquisition and therefore does not contribute to growth (Fig. 1a).

What swimming speed to choose?

Given the metabolic costs of aerobic swimming, and how these change with speed, the question that arises is what speed to impose in order to enhance or promote growth. The currents or swimming speeds reported to give the best growth of fishes, primarily based on studies of salmonids, are in the range of 0.5-1.7 $bl \cdot s^{-1}$ (Davison, 1997, 1989; Davison and Herbert, 2013; Jobling et al., 1993). Based on data from a number of salmonids and carangids, Davison and Herbert (2013) proposed that the swimming speed at which optimal growth occurs should coincide with the U_{opt} (see Fig 8.4, Davison and Herbert, 2013). This raises the complicating factor of fish length, since smaller fishes swim at higher relative speeds and therefore have higher U_{opt} when normalised to $BL \cdot s^{-1}$ (Davison and Herbert, 2013). The importance of size-related differences in U_{opt} has not received sufficient attention but is clearly of potential significance for applying exercise as a tool in aquaculture, including in

terms of adjusting speeds as fishes grow. From the literature, it is evident that a large number of studies on effects of exercise on growth have been conducted on small fishes (Table 8.1 Davison and Herbert, and Table 1). This is a logical consequence of issues such as limited laboratory space, numbers and sizes of available tanks, and the cost of animals and feed, but means that much available information is about juveniles rather than animals approaching marketable size.

Fishes are active even when there is no current

The swimming speed of fishes is not always determined by the water current. Even if kept in still water, many species of fish will swim spontaneously and, under these conditions, their metabolic rate may be increased (Fig 2) to the extent that it is either equal to (Christiansen et al., 1991) or higher than that of fish swimming steadily against a moderate current (Skov et al., 2011). In fact, swimming spontaneously with a complex turning trajectory can be significantly more costly than swimming at the same speed but against a current and in a straight line (Steinhausen et al., 2010). If not compensated for by increased energy intake, the increased metabolic rate would reduce growth (Fig. 2). In still water or at very low swimming speeds, increased activity levels of fishes can reflect increased levels of aggression, which disappear when a current is provided that stimulates shoaling or schooling (Christiansen and Jobling, 1990; Christiansen et al., 1989; East and Magnan, 1987; Jørgensen and Jobling, 1993). Aggression can result in reduced feed intake (Christiansen and Jobling, 1990; Jørgensen and Jobling, 1993) and, as a result, reduced growth compared with fish swimming against a current at moderate velocities (Fig. 2). The spontaneous behaviour and aggressivity of fishes also depends on other factors, such as rearing density (Christiansen et al., 1991; Jørgensen et al., 1993; Larsen et al., 2012; McKenzie et al., 2012) and access to feed (Jørgensen et al., 1996), which can also affect their growth (Jobling et al., 1993). Overall, spontaneous swimming behaviour of fishes may be a significant factor in determining how a current influences growth rates (Christiansen and Jobling, 1990; Larsen et al., 2012; McKenzie et al., 2012; Skov et al., 2015).

Mechanisms for increased growth

It is possible that, in many studies, the positive effects of exercise on growth were simply derived from an increase in feed intake. In many early studies, feeding was unrestricted and feed intake was not reported, such that feed efficiency and FCR are not known. In this regard, it is interesting that beneficial effects of swimming exercise are often found when comparing

fish kept in still water and those swimming at intermediate swimming velocities, 0.5 to 2 BL s⁻¹ (Davison and Herbert, 2013). Swimming exercise can stimulate appetite (Fig. 2) to match the increased metabolic demands of locomotion, such that growth is not compromised or is even increased (Christiansen and Jobling, 1990; Jørgensen and Jobling, 1993; Khan et al., 2014; Leon, 1986; Li et al., 2016; Skov et al., 2015; Totland et al., 1987). In fact, fish species may be able to exercise constantly at velocities between 0.5 to 2 BL s⁻¹ without any decline in growth rate, by compensating with increased feed intake. This, of course, implies progressively reduced feed efficiency and FCR as swimming speed increases (Kießling et al., 1994, 2005; Khan et al., 2014; Skov et al., 2015; Table 1).

It is conceivable, nonetheless, that FCR and growth ‘efficiency’ are improved in exercised fish compared with those held in still water (Christiansen and Jobling, 1990; Jobling et al., 1993; Shrivastava et al., 2018). Swimming exercise at moderate levels appears to stimulate various regulatory factors that affect feed intake or growth, such as the expression of growth hormone (GH) and insulin-like growth factor-1 (IGF-1) (Barrett and McKeown, 1988; Blasco et al., 2015; Shrivastava et al., 2018) as well as expression of various genes associated with growth processes (Palstra et al., 2010b). Moreover, protein turnover and deposition have been reported to increase in exercised fish compared with controls in still water (Houlihan and Laurent, 1987). It is also true, however, that improved FCR of fishes reared at moderate swimming speeds, compared with those in still water, could also result from reduced feed intake and/or higher metabolic rates of the latter group, for the behavioural reasons that we have outlined above. Indeed, few if any studies showing increased growth rates in moderately exercised fish have included detailed measurements of feed intake and metabolic rate.

Future directions and considerations

It is clear that further work is needed to understand how swimming exercise can be used to improve production in aquaculture. There is no consensus in the literature and it is not clear to what extent this reflects differences among species, in life stage and body size, in the swimming speed applied, the feeding regime, and so forth. Feed represents the major operational cost in fish farming and, in many instances, production is regulated by feed quotas or nutrient emission allowances. From this perspective, increased growth is only really interesting if it is linked to more efficient utilization of ingested feed. Thus, further research is needed to demonstrate that aerobic swimming improves FCR or protein retention in the

species of interest, throughout rearing to market size. The best advice for which swimming speed to choose remains that this should be close to U_{opt} (Davison and Herbert, 2013).

Research efforts on the effects of exercise should also consider diet formulation, in particular to increase non-protein energy to fuel the metabolic costs of swimming, such that dietary protein can be retained and allocated towards growth. Magnoni et al. (2013) emphasized the need for research into how dietary lipids and carbohydrates are used to fuel sustained swimming in fishes. There have been some studies investigating how swimming fish use fuels (Kieffer et al., 1998; Lauff and Wood, 1997; Liew et al., 2012; Richards et al., 2002). The work of Alsop and Wood (1997) demonstrated an increased reliance on non-protein energy sources to fuel metabolism with increasing swimming speeds in rainbow trout (*Oncorhynchus mykiss*). Skov et al. (2015) made a similar observation, noting that the nitrogen quotient in rainbow trout was reduced by 20% in trout swimming against a current at 1 BL s^{-1} , compared to trout held in still water (0 BL s^{-1}). Although this was beneficial in reducing the relative reliance on protein as fuel, overall fuel use was higher in the trout held in a swimming current. Interestingly, carbohydrate may contribute 40% of the metabolic cost of swimming at intermediate speeds, despite carbohydrate only making up ~10% of the energy reserves of a fish (Magnoni et al., 2013). In studies by Ibarz et al. (2011) and Sánchez-Gurmaches et al. (2013), an increase in dietary carbohydrate content had beneficial effects on the growth of gilthead seabream (*Sparus aurata*) reared with a swimming current. This may be linked to increased uptake and use of carbohydrates as fuel in skeletal muscle, which promotes a protein-sparing effect, as reported for rainbow trout (Felip et al., 2012; Skov et al., 2015). Nutritional optimisation is, therefore, a topic that is certainly worthy of further investigation.

Exercise and mitigation: links with welfare

Welfare is an extremely important element of successful intensive aquaculture, being a broad concept that embraces both the physical and mental well-being of an animal. A pragmatic definition of 'good welfare' is that an animal is healthy and has what it 'wants' (Dawkins 2008). This definition encompasses the three alternative definitions of animal welfare (Fraser, 2008) based on function, feelings and nature, where animals should have positive natural experiences similar to those in the wild. In food production aquaculture, the function-based definition tends to dominate (Huntingford et al., 2006), whereby basic biological functions like health, growth and reproduction are optimised under rearing conditions. There are a

number of ways in which sustained aerobic exercise may promote welfare of farmed fishes, in terms of physical and mental well-being, and managing reproductive physiology.

Exercise and stress

There has been significant interest in whether exercise can improve welfare of intensively farmed fishes by alleviating stress, encouraged by the evidence that moderate aerobic exercise can provide relief against stress in mammals and humans (Eliot et al., 1976; Tsatsoulis and Fountoulakis, 2006). Stress, in its strictest sense, is an endocrine condition that indicates activation of the hypothalamic-pituitary axis that, in fishes, elicits a release of the steroid stress hormone cortisol. Stress can also, however, have a broader definition than the endocrine stress response; it can be considered to comprise any condition that causes deviations from homeostasis that can engender a decline in performance and welfare of animals (Schreck and Tort, 2016; Schulte, 2014). Therefore, markers of ‘stress’ can include increased metabolic energy (and hence oxygen) demands or deviations in blood chemistry homeostasis, and reductions in ‘fitness indicators’ such as swimming performance itself, growth rates or tolerance of disease (Schreck and Tort, 2016; Schulte, 2014). For fishes in aquaculture, it is widely recognised that factors such as non-optimal stocking densities or the formation of dominance hierarchies can cause chronic stress (Barton and Iwama, 1991; Schreck and Tort, 2016). It has also been suggested that not allowing active fishes, such as salmonids, the option to exercise against a current may, in itself, be intrinsically stressful (Rodnick and Planas, 2016).

Various studies have investigated whether providing a current to swim against can alleviate chronic stress in active fish species when reared in tanks, assessed as a reduction in circulating cortisol levels in blood. Table 2 shows the studies which have investigated how sustained aerobic exercise influences plasma cortisol in fishes. There is no clear picture that emerges, with exercise causing decreases, no change or even increases in circulating cortisol. Clearly, the different responses may reflect the different species, current speeds and holding conditions, and the existing data allow no conclusions to be drawn about the potential impact of such factors. There is also an enduring debate about how to interpret plasma cortisol levels in fishes because of the complex feedback loops that can occur within endocrine responses (Barton et al., 2005; Schreck and Tort, 2016).

It can be informative to evaluate how fish rearing conditions influence the ability to mount an acute stress response, as this reveals whether the HPI axis might have been

downregulated by chronic stress (Schreck and Tort, 2016). In the striped bass (*Morone saxatilis*), swimming lowered circulating levels of cortisol (Table 2) but did not influence the magnitude of the cortisol response to an acute handling stress (Young and Cech Jr., 1993). In rainbow trout, sustained swimming either lowered (Woodward and Smith, 1985) or did not affect (McKenzie et al., 2012) circulating cortisol titres (Table 2) but, in both studies, there was no significant effect of swimming on the magnitude of the cortisol response to an acute stress. In matrinxà (*Brycon amazonicus*), sustained swimming lowered plasma cortisol titres (Arbelaez-Rojas et al., 2017), although it had no effect on their cortisol response to transport stress (Arbeláez-Rojas et al., 2013). Thus, the evidence indicates that swimming has no chronic effects on sensitivity of the HPI axis to acute stress (Table 2..

There is strong evidence, however, that providing a current to swim against can accelerate recovery of plasma cortisol homeostasis after acute stresses such as exercise to exhaustion (Milligan et al., 2000), handling (Young and Cech Jr., 1993), confinement (McKenzie et al., 2012; Veiseth et al., 2006) or live transport (Arbelaez-Rojas et al., 2017). Interestingly, the evidence that providing a current promotes more rapid recovery of plasma metabolites following exercise to exhaustion is more mixed. In some studies and species it did (e.g. Lackner et al., 1988; Milligan et al., 2000; Veiseth et al., 2006) whereas, in others, it did not (Kieffer et al., 2011; Meyer and Cook, 1996; Suski et al., 2015). Exercise to exhaustion causes profound metabolic disturbances and should very rarely (or never) occur in aquaculture. The accelerated recovery of cortisol might be a training effect, where fishes that are exercised for extended periods develop greater scope for metabolism, that allows them to recover general homeostasis more rapidly (Lackner et al., 1988; McKenzie et al., 2012).

To conclude, there is no clear support for the notion that providing a current during rearing can systemically alleviate endocrine ‘stress’ in fishes. A swimming current may, however, mitigate routine handling and transport stresses, by accelerating recovery of endocrine homeostasis.

Exercise and immunity

There is very limited knowledge regarding the impact of exercise regimes on the immune performance of farmed fishes, but this is an interesting area for research because of the severe impacts that disease can have on aquaculture operations. In mammals, it is now generally accepted that aerobic exercise improves immunocompetency, although intense exhaustive exercise may be immunosuppressive (Campbell and Turner, 2018). In various mammalian

species including humans, exercise influences disease resistance, the capacity to initiate a successful immune response to pathogens, and vaccination success (Pascoe et al., 2014). One underlying mechanism may be that aerobic exercise stimulates leucocytosis and redistribution of leukocytes throughout the body. This redistribution has been linked to a heightened state of immune surveillance and immune regulation, which contributes to an increased resistance to infection (Campbell and Turner, 2018).

In fishes, Castro et al. (2013) reported that Atlantic salmon (*Salmo salar*) individuals with inherently good swimming performance displayed increased resistance to a viral infection, infectious pancreatic necrosis virus (IPNV). In the same experiment different training regimes did not, however, improve immune performance. That is, individual variation in swimming performance accounted for variation in disease resistance, rather than a training regime. A further study compared immune-related gene profiles in a wild versus a domesticated population of Atlantic salmon, that had been further classified into inferior or superior swimmers. This revealed complex differences in gene expression between the populations but there was no link to inherent swimming performance nor any specific pattern of response to the training regime (Robinson et al., 2017).

In mammals, it is highly likely that cell mobilisation and redistribution throughout the body during exercise significantly contributes to any subsequent changes in tissue immune-related gene expression (Campbell and Turner, 2018). It has proven difficult to understand the tissue distribution of the various cells of the immune response, and their capacity for mobilisation and redistribution (Campbell and Turner, 2018; Hay and Andrade, 1998). Thus, if gene expression data from mammals must be interpreted with caution, the situation is even less favourable for studies of effects of exercise on fishes. There is a very limited toolbox for accurate cellular phenotyping to analyse populations of leukocytes and their tissue distributions. This, coupled with our limited understanding of immune system dynamics during exercise, represents a bottleneck in our current capacity to interpret data in fishes.

It is worthwhile to mention that exercise, both acute and chronic, has a beneficial adjuvant-type effect on the immune response to vaccination in mammals (Pascoe et al, 2014). Interestingly, this has been attributed to cytokine release including interleukin-6 (IL-6), and to tissue damage, particularly muscle damage (Bruunsgaard et al., 1997). A recent study in zebrafish (*Danio rerio*) identified increased expression of IL-6 in certain muscle fibres in response to exercise (Rovira et al., 2017). These observations suggest that exercise regimes

may have potential to increase the effectiveness of vaccination in commercially farmed fish species, by a similar beneficial adjuvant-like effect.

Exercise, cognition and neural plasticity

Given the desire to ensure optimal welfare in intensively-farmed fishes, there has been interest in whether stimulating aerobic exercise with a current can promote neurogenesis, neuroplasticity and cognition (Huntingford and Kadri, 2013). Such effects of exercise are well-established in mammals (Cotman and Berchtold, 2002; van Praag, 2008). In adult rodents, for example, voluntary exercise promotes neurogenesis and expression of neurotrophins, particularly in the hippocampus (Cotman and Berchtold, 2002; Soya et al., 2007). The hippocampus plays an important role in relational memory and spatial orientation (Broglia et al., 2015) and exercised mammals show increased cognitive performance in maze tests compared to sedentary conspecifics (Ma et al., 2017; van Praag, 2008; Vaynman et al., 2004). While neurogenesis in the adult mammalian brain occurs at relatively low rates and only in discrete brain areas, fishes exhibit neurogenesis in a multitude of brain areas throughout their lifespan (Zupanc, 2006; Zupanc and Sîrbulescu, 2011). This fact was a particular stimulus for investigating whether exercise-induced enhancement of neurogenesis and cognition also occurs in fishes (Huntingford and Kadri, 2013).

Recent studies have confirmed that exercise can promote neurogenesis and neuroplasticity in juvenile Atlantic salmon. Eight weeks of voluntary sustained swimming caused upregulation of genes involved with neuronal signalling, cell proliferation and neurite outgrowth in the telencephalon transcriptome (Mes et al., 2020). Furthermore, increased expression of a neurogenesis marker, *proliferating cell nuclear antigen (pcna)*, plus two neuroplasticity markers, *synaptotagmin (syt)* and *brain-derived neurotrophic factor (bdnf)*, was found in specific areas of the telencephalon in the exercised group (Mes et al., 2020). In the brain of zebrafish larvae, a six-day intermittent training regime increased expression of two genes involved in neurogenesis, cell differentiation and cell growth (Fiaz et al., 2014). Interestingly, exercise-enhanced expression of neuroplasticity markers has been observed in multiple areas of the telencephalon of exercised fish and does not seem to be confined to the dorsolateral pallium, which in fishes is the functional equivalent of the mammalian hippocampus.

To date, little is known about the effects of swimming exercise on cognition in fishes. A 20-day exhaustive swimming exercise regime improved associative learning performance

in a conditioning test in zebrafish (Luchiari and Chacon, 2013). However, neither three nor eight weeks of voluntary sustained swimming improved the cognitive performance of Atlantic salmon parr in a maze test, despite increased expression of neuroplasticity markers in their telencephalon (Mes et al., 2018).

Overall, the existing findings suggest that, although exercise can promote neural plasticity in teleosts, there is little evidence for an associated increase in cognition. This is an interesting area for future research, in particular with a comprehensive approach that evaluates both neuroplasticity markers and cognitive performance in the same experiment. A particular focus should be upon enhancing cognition in animals that will be used in stocking programs, because hatchery-reared fish are often behaviourally naïve and consequently have low survival rates when released into the wild (Jonsson and Jonsson, 2009; Thorstad et al., 2011).

Exercise and sexual maturation

Precocious maturation is a significant problem for many important aquaculture species, notably European sea bass (*Dicentrarchus labrax*) (Felip et al., 2008), gilthead seabream (Gines et al., 2003), Atlantic cod (*Gadus morhua*) (Taranger et al., 2006) and Atlantic salmon (Good and Davidson, 2016). As fishes grow, the transition from the juvenile phase, characterised by extensive somatic growth, to a mature adult phase characterized by gonadal recrudescence and spawning, involves a major change in patterns of energy allocation. Energy investments in early maturation may negatively impact growth performance, feed conversion efficiency, fillet quality and the development of the immune system and, consequently, cause important economic losses.

Although the exact mechanisms that trigger this transition in energy allocation are still not known, it has been suggested that swimming exercise may play an important role in suppressing sexual maturation. This is because fish species that exhibit lengthy reproductive migrations show delayed or even arrested gonadal development during the migration itself. Such long-distance migrants show swimming-induced suppression of ovarian development at the start of vitellogenesis (or puberty), which may be a strategy to avoid increased drag resistance due to oocyte growth and to prevent precocious muscle atrophy. When female European eels (*Anguilla anguilla*) were subjected to long-term sustained exercise, declines in mRNA expression of estrogen receptor 1, vitellogenin1 and vitellogenin2 in the liver indicated suppression of hepatic vitellogenesis (Palstra et al., 2010a; Palstra and van den Thillart, 2010). Furthermore, when appropriate photothermal conditions were mimicked

during a simulated migration, European eel ovaries advanced their previtellogenic development but did not initiate vitellogenesis (Mes et al., 2016). Female rainbow trout subjected to long-term exercise showed suppressed oocyte development, possibly through inhibition of vitellogenin uptake (Palstra et al., 2010a). A concomitant downregulation of transcriptomic responses in the ovary indicated that the energetic strategy was focussed on migration rather than sexual maturation. Thus, sustained exercise can delay gonadal development in various migratory fish species.

This has stimulated research into whether a sustained exercise regime can prevent precocious maturation in farmed fishes. Graziano et al. (2018) showed that exercise at U_{opt} resulted in delayed testicular development in male European sea bass. The gonado-somatic index was lower, testicular development was delayed and the expression of genes involved in testicular development was down-regulated in exercised as compared to non-exercised fish. Waldrop et al. (2018) found that male Atlantic salmon exercised at swimming speeds of 1.5 to 2.0 BL s^{-1} showed significantly less precocious maturation than those swimming at a speed lower than 0.5 BL s^{-1} (6.5% and 11.5%, respectively).

Therefore, exercise may be a promising tool to reduce the incidence of sexual precociousness in aquaculture and this is a particularly interesting area for future research. Notably, to investigate fundamental questions such as the mechanisms by which sustained aerobic exercise suppresses sexual maturation in fishes. For example, in coho salmon (*Oncorhynchus kisutch*) and rainbow trout (Barrett and McKeown, 1989, 1988), exercise can enhance plasma levels of GH and, in gilthead seabream, it raises plasma IGF-I levels (Sánchez-Gurmaches et al., 2013). This stimulation of growth factors may prevent the transition from a juvenile life stage, governed by the GH/IGF axis, to a reproductive stage governed by the brain-pituitary-gonadal axis, a switch that is often preceded by a drop in GH.

Swimming behaviours as Operational Welfare Indicators

Swimming and the activities that it underpins are obviously natural behaviours that can promote 'good welfare' so, ideally, captive fishes should be allowed to express them without restrictions. Behavioural swimming patterns and responses are good OWI that provide information about the welfare of groups of fish under culture conditions, rather than about single individuals. Swimming activity provides good OWI that, for a given species, may comprise different patterns and space requirements at different life stages. The movement and orientation of larvae can provide guidance for welfare, especially during weaning when it can

reflect yolk sac depletion and first feeding. A good OWI would be the proportion of fish orientating and migrating to the surface to feed actively. Fishes start swimming actively after weaning and, therefore, swimming patterns in the tank, alongside horizontal and vertical distributions, are also a useful OWI. Interpreting movement patterns requires knowledge of the species, Shoaling or schooling in the tank may indicate good welfare, rather than chaotic movements and clumped distribution indicative of anxiety like behaviour and stress responses. Tight shoals can, however, be induced by fear of predation, which may indicate an underlying stress response. In tank systems for salmonids, the water flow rate should ideally allow the fish to 'hold station', a natural behaviour for these species. Increasing the flow rate so that fish shoal and swim actively against a current can also mitigate against agonistic behaviours, as discussed earlier. This provides an OWI because agonistic behaviours can reduce welfare by causing stress and fin damage (Jobling et al., 1993).

Exercise and selection: creating more robust strains?

Little is known about the genetic basis of swimming performance in fishes, and whether there might be genetic correlations with traits of interest for production. In terrestrial livestock, selection for production traits has been shown to lead to various disorders including cardiac failures in intensely selected lines (Nestor et al., 1996; Rauw et al., 1998). Thus, it has been suggested that the occurrence of cardiac malformations and failures in some lines of farmed salmonids (Mercier et al., 2000; Poppe et al., 2007) could similarly be linked to prioritising growth rate in selective breeding. In rainbow trout selected for rapid growth, individual swimming performance was a predictor of cardiac morphology and pumping ability (Claireaux et al., 2005). It has been suggested, therefore, that swimming performance phenotype could potentially be selected upon, to improve the functional integrity of farmed fish that have previously been selected for rapid growth. There are, however, very few studies that have investigated the genetic basis of swimming ability.

Heritability measures the fraction of phenotypic variance that can be attributed to genetic variation and ranges from 0 (none can be attributed) to 1 (all is attributed). In brown trout (*Salmo trutta*) and Atlantic salmon, heritability of U_{crit} was moderate with large error terms, namely 0.34 ± 0.22 (Blanc and Toulorge, 1981) and 0.24 ± 0.16 (Hurley and Schom, 1984), respectively. Similar heritability estimates of 0.24 ± 0.19 were reported for the guppy *Poecilia reticulata* Peters 1859 (Nicoletto, 1995). In the threespine stickleback *Gasterosteus aculeatus* L. 1756, heritability of burst swimming speed was relatively high at two months of

age (0.37-0.41) but had fallen to almost zero at 3.6 months in the same individuals, raising questions about the validity of the results (Garenc et al., 1998). In the European sea bass, heritability of relative maximum burst swimming speed (in BL s⁻¹) was quite high, at 0.55 ± 0.08 (Vandeputte et al., 2016), with a very high (0.96) genetic correlation between two independent evaluations of the trait, on the same fish at 5-day intervals.

Genetic correlations between swimming performance and other traits have been studied very little. There were weak positive correlations (0.23) between absolute maximum sustained swimming speed and body mass in Atlantic salmon (Hurley and Schom, 1984) and in European sea bass (0.12; Vandeputte et al., 2016). In European sea bass, maximum swimming speed in BL s⁻¹ was negatively correlated with body mass, and this was true of all genetic (-0.64), phenotypic (-0.56) and environmental (-0.45) correlations (Vandeputte et al., 2016). This suggests that the negative relationship between body size and relative swimming speed is purely phenotypic, as has already been established in fishes (Bainbridge, 1958; Beamish, 1978; Bellwood & Fisher, 2001). In European sea bass, there was a weak negative genetic correlation (-0.10 ± 0.19) but no phenotypic correlation (0.01) between relative swimming speed and cortisol response to confinement stress, indicating that these two traits are independent in this species (Vandeputte et al., 2016). The same study also found no difference in relative or absolute swimming speed between the offspring of wild, domesticated (1 generation) or growth selected (1 generation) parents, confirming moderate links between swimming capacity and the genetic bases of growth.

Thus, keeping in mind what has been observed in terrestrial livestock, it is possible that selection for growth degrades swimming ability and underlying cardiac performance, over successive generations, but further investigation is needed to demonstrate genetic links between these traits. Nonetheless, due to the moderate to high heritability of swimming capacity, selecting fish for improved exercise performance could be a simple way to counteract any negative effects of selection for fast growth. It may also be a means of ensuring that robust animals with good exercise performance are used in restocking programs, to promote their survival (Jobling et al., 1993; Thorstad et al., 2011).

Conclusions

Despite a great deal of interest from the aquaculture research community, it remains to be explicitly demonstrated that swimming exercise can actually 'promote' growth and improve feed efficiency, except through modifications to behaviour. There is also no consensus about

whether swimming exercise can mitigate chronic stress in all species. Whether exercise can promote immunity and cognition is an interesting question that is worth exploring further, because there are clear potential applications in terms of welfare of farmed fishes. The evidence that exercise can inhibit precocious sexual maturation is also very promising, so this is another area where research should be encouraged. The use of swimming behaviour as OWI is of clear potential value to the fish farmer, especially for early life stages, so further studies on a broader range of species would be valuable. Finally, using exercise to select robust phenotypes, or to counteract debilitating effects of a historical selection for rapid growth, also requires further investigation. Overall, therefore, further research is required, in concert with fish farmers, to develop methods to exercise fishes in culture, or to use exercise as a selection tool.

REFERENCES

- 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.
- Arbeláez-Rojas, G.A., Hackbarth, A., Inoue, L.A.K.A., Dias de Moraes, F., Moraes, G., 2013. Sustained Swimming Mitigates Stress in Juvenile Fish *Brycon amazonicus*. *J. Appl. Aquac.* 25, 271–281. <https://doi.org/10.1080/10454438.2013.817198>
- Arbelaez-Rojas, G.A., Moraes, G., Nunes, C. da S., Fabrizzi, F., 2017. Sustained swimming mitigates stress in juvenile *Brycon amazonicus* reared in high stocking densities. *Pesqui. Agropecu. Bras.* 52, 1–9. <https://doi.org/10.1590/S0100-204X2017000100001>
- Bainbridge, R., 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *J. Exp. Biol.* 35, 109–133.
- Barrett, B.A., McKeown, B.A., 1989. Plasma growth hormone levels in *Salmo gairdneri*: Studies on temperature and the exercise intensity/duration relationship. *Comp. Biochem. Physiol. Part A Physiol.* 94, 791–794. [https://doi.org/10.1016/0300-9629\(89\)90635-X](https://doi.org/10.1016/0300-9629(89)90635-X)
- Barrett, B.A., McKeown, B.A., 1988. Sustained Exercise Increases Plasma Growth Hormone Concentrations in Two Anadromous Salmonids. *Can. J. Fish. Aquat. Sci.* 45, 747–749. <https://doi.org/10.1139/f88-091>
- Barton, B.A., Iwama, G.K., 1991. Physiological changes in fish from stress in aquaculture

- with emphasis on the response and effects of corticosteroids. *Annu. Rev. Fish Dis.* 1, 3–26. [https://doi.org/10.1016/0959-8030\(91\)90019-G](https://doi.org/10.1016/0959-8030(91)90019-G)
- Barton, B.A., Ribas, L., Acerete, L., Tort, L., 2005. Effects of chronic confinement on physiological responses of juvenile gilthead sea bream, *Sparus aurata* L., to acute handling. *Aquac. Res.* 36, 172–179. <https://doi.org/10.1111/j.1365-2109.2004.01202.x>
- Beamish, F.W.H., 1978. Swimming capacity, in: Hoar, W.S., Randall, D.J. (Eds.), *Fish Physiology Volume 7*. Academic Press, New York, pp. 101–187.
- Bellwood, D., Fisher, R., 2001. Relative swimming speeds in reef fish larvae. *Mar. Ecol. Prog. Ser.* 211, 299–303.
- Blanc, J., Toulorge, J., 1981. Variabilité génétique de la performance de nage chez l’alevin de Truite fario (*Salmo trutta*). *Genet. Sel. Evol.* 13, 165. <https://doi.org/10.1186/1297-9686-13-2-165>
- Blasco, F.R., Esbaugh, A.J., Killen, S., Rantin, F.T., Taylor, E.W., McKenzie, D.J., 2020. Using aerobic exercise to evaluate sub-lethal tolerance of acute warming in fishes. *J. Exp. Biol.* 223: jeb218602 doi: 10.1242/jeb.218602
- Blasco, J., Moya, A., Millán-Cubillo, A., Vélez, E.J., Capilla, E., Pérez-Sánchez, J., Gutiérrez, J., Fernández-Borrás, J., 2015. Growth-promoting effects of sustained swimming in fingerlings of gilthead sea bream (*Sparus aurata* L.). *J. Comp. Physiol. B* 185, 859–868. <https://doi.org/10.1007/s00360-015-0933-5>
- Boesgaard, L., Nielsen, M.E., Rosenkilde, P., 1993. Moderate exercise decreases plasma cortisol levels in atlantic salmon (*Salmo salar*). *Comp. Biochem. Physiol. -- Part A Physiol.* 106, 641–643. [https://doi.org/10.1016/0300-9629\(93\)90373-C](https://doi.org/10.1016/0300-9629(93)90373-C)
- Brett, J.R., 1976. Scope for Metabolism and Growth of Sockeye Salmon, *Oncorhynchus nerka*, and Some Related Energetics. *J. Fish. Res. Board Canada* 33, 307–313. <https://doi.org/10.1139/f76-046>
- Brett, J.R., Groves, T.D.D., 1979. Physiological Energetics, in: Hoar, W.S., Randall, D.J., Brett, J.R. (Eds.), *Fish Physiology Volume 8*. Academic Press, New York, pp. 280–352.
- Broglio, C., Martín-Monzón, I., Ocaña, F.M., Gómez, A., Durán, E., Salas, C., Rodríguez, F., 2015. Hippocampal Pallium and Map-Like Memories through Vertebrate Evolution. *J. Behav. Brain Sci.* 5, 109–120. <https://doi.org/10.4236/jbbs.2015.53011>
- Brown, E.J., Bruce, M., Pether, S., Herbert, N.A., 2011. Do swimming fish always grow fast? Investigating the magnitude and physiological basis of exercise-induced growth in

- juvenile New Zealand yellowtail kingfish, *Seriola lalandi*. *Fish Physiol. Biochem.* 37, 327–336.
- Brunnsgaard, H., Galbo, H., Halkjaer-Kristensen, J., Johansen, T.L., MacLean, D.A., Pedersen, B.K., 1997. Exercise-induced increase in serum interleukin-6 in humans is related to muscle damage. *J. Physiol.* 499, 833–841.
<https://doi.org/10.1113/jphysiol.1997.sp021972>
- Burgetz, I., Rojas-Vargas, A., Hinch, S., Randall, D., 1998. Initial recruitment of anaerobic metabolism during sub-maximal swimming in rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* 201.
- Cai, L., Fang, M., Johnson, D., Lin, S., Tu, Z., Liu, G., Huang, Y., 2014. Interrelationships between feeding, food deprivation and swimming performance in juvenile grass carp. *Aquat. Biol.* 20, 69–76. <https://doi.org/10.3354/ab00546>
- Campbell, J.P., Turner, J.E., 2018. Debunking the Myth of Exercise-Induced Immune Suppression: Redefining the Impact of Exercise on Immunological Health Across the Lifespan. *Front. Immunol.* 9, 648. <https://doi.org/10.3389/fimmu.2018.00648>
- Castro, V., Grisdale-Helland, B., Helland, S.J., Kristensen, T., Jørgensen, S.M., Helgerud, J., Claireaux, G., Farrell, A.P., Krasnov, A., Takle, H., 2011. Aerobic training stimulates growth and promotes disease resistance in Atlantic salmon (*Salmo salar*). *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* 160, 278–290.
<https://doi.org/10.1016/j.cbpa.2011.06.013>
- Castro, V., Grisdale-Helland, B., Jørgensen, S.M., Helgerud, J., Claireaux, G., Farrell, A.P., Krasnov, A., Helland, S.J., Takle, H., 2013. Disease resistance is related to inherent swimming performance in Atlantic salmon. *BMC Physiol.* 13, 1.
<https://doi.org/10.1186/1472-6793-13-1>
- Christiansen, J., Jobling, M., 1990. The behaviour and the relationship between food intake and growth of juvenile Arctic charr, *Salvelinus alpinus* L., subjected to sustained exercise. *Can. J. Zool.* 68, 2185–2191.
- Christiansen, J.S., Jørgensen, E.H., Jobling, M., 1991. Oxygen-Consumption in Relation to Sustained Exercise and Social Stress in Arctic Charr (*Salvelinus-Alpinus* L). *J. Exp. Zool.* 260, 149–156. <https://doi.org/10.1002/jez.1402600203>
- Christiansen, J.S., Ring, E., Jobling, M., 1989. Effects of Sustained Exercise on Growth and Body Composition of First-Feeding Fry of Arctic Charr, *Salvelinus alpinus* (L.) 79,

329–335.

- Claireaux, G., Couturier, C., Groison, A.-L., 2006. Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (*Dicentrarchus labrax*). *J. Exp. Biol.* 209, 3420–8. <https://doi.org/10.1242/jeb.02346>
- Claireaux, G., McKenzie, D.J., Genge, a G., Chatelier, A., Aubin, J., Farrell, A.P., 2005. Linking swimming performance, cardiac pumping ability and cardiac anatomy in rainbow trout. *J. Exp. Biol.* 208, 1775–84. <https://doi.org/10.1242/jeb.01587>
- Cotman, C.W., Berchtold, N.C., 2002. Exercise: a behavioral intervention to enhance brain health and plasticity. *Trends Neurosci.* 25, 295–301. [https://doi.org/10.1016/S0166-2236\(02\)02143-4](https://doi.org/10.1016/S0166-2236(02)02143-4)
- Davison, W., 1997. The Effects of Exercise Training on Teleost Fish , a Review of Recent Literature 117, 67–75.
- Davison, W., 1989. Training and its effects on teleost fish. *Comp. Biochem. Physiol. Part A Physiol.* 94, 1–10. [https://doi.org/10.1016/0300-9629\(89\)90775-5](https://doi.org/10.1016/0300-9629(89)90775-5)
- Davison, W., Goldspink, G., 1977. The effect of prolonged exercise on the lateral musculature of the brown trout (*Salmo trutta*), *J. Exp. Biol.*
- Davison, W., Herbert, N.A., 2013. Swimming-Enhanced Growth, in: *Swimming Physiology of Fish*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 177–202. https://doi.org/10.1007/978-3-642-31049-2_8
- Dawkins, M.S., 2008. The Science of Animal Suffering. *Ethology* 114, 937–945. <https://doi.org/10.1111/j.1439-0310.2008.01557.x>
- East, P., Magnan, P., 1987. The effect of locomotor activity on the growth of brook charr, *Salvelinus fontinalis* Mitchill. *Can. J. Zool.* 65, 843–846. <https://doi.org/10.1139/z87-134>
- Eliot, R.S., Forker, A.D., Robertson, R.J., 1976. Aerobic exercise as a therapeutic modality in the relief of stress. *Adv. Cardiol.* 18, 231–42. <https://doi.org/10.1159/000399527>
- Felip, A., Zanuy, S., Muriach, B., Cerdá-Reverter, J.M., Carrillo, M., 2008. Reduction of sexual maturation in male *Dicentrarchus labrax* by continuous light both before and during gametogenesis. *Aquaculture* 275, 347–355. <https://doi.org/10.1016/J.AQUACULTURE.2008.01.020>
- Felip, O., Blasco, J., Ibarz, A., Martin-Perez, M., Fernández-Borràs, J., 2012. Beneficial effects of sustained activity on the use of dietary protein and carbohydrate traced with stable isotopes ¹⁵N and ¹³C in gilthead sea bream (*Sparus aurata*). *J. Comp. Physiol. B*

- 183, 223–234. <https://doi.org/10.1007/s00360-012-0703-6>
- Felip, O., Ibarz, A., Fernández-Borràs, J., Beltrán, M., Martín-Pérez, M., Planas, J. V., Blasco, J., 2012. Tracing metabolic routes of dietary carbohydrate and protein in rainbow trout (*Oncorhynchus mykiss*) using stable isotopes ($[^{13}\text{C}]$ starch and $[^{15}\text{N}]$ protein): Effects of gelatinisation of starches and sustained swimming. *Br. J. Nutr.* 107, 834–844. <https://doi.org/10.1017/S0007114511003709>
- Fiaz, A.W., Léon-Kloosterziel, K.M., van Leeuwen, J.L., Kranenbarg, S., 2014. Exploring the effect of exercise on the transcriptome of zebrafish larvae (*Danio rerio*). *J. Appl. Ichthyol.* 30, 728–739. <https://doi.org/10.1111/jai.12509>
- Fitzgibbon, Q.P., Strawbridge, A., Seymour, R.S., 2007. Metabolic scope, swimming performance and the effects of hypoxia in the mulloway, *Argyrosomus japonicus* (Pisces: Sciaenidae). *Aquaculture* 270, 358–368. <https://doi.org/10.1016/j.aquaculture.2007.04.038>
- Forster, I.P., Ogata, H., 1996. Growth and Whole-body Lipid Content of Juvenile Red Sea Bream Reared under Different Conditions of Exercise Training and Dietary Lipid. *Fish. Sci.* 62, 404–409. <https://doi.org/10.2331/fishsci.62.404>
- Fraser, D., 2008. Understanding animal welfare. *Acta Vet. Scand.* 50, S1. <https://doi.org/10.1186/1751-0147-50-S1-S1>
- Gallaughan, P.E., Thorarensen, H., Kiessling, a, Farrell, A. P., 2001. Effects of high intensity exercise training on cardiovascular function, oxygen uptake, internal oxygen transport and osmotic balance in chinook salmon (*Oncorhynchus tshawytscha*) during critical speed swimming. *J. Exp. Biol.* 204, 2861–72.
- Garenc, C., Silversides, F.G., Guderley, H., 1998. Burst swimming and its enzymatic correlates in the threespine stickleback (*Gasterosteus aculeatus*): full-sib heritabilities. *Can. J. Zool.* 76, 680–688. <https://doi.org/10.1139/z97-236>
- Ghanawi, J., Mohanna, C., Saoud, I.P., 2010. Effect of continuous water movement on growth and body composition of Juvenile rabbitfish, *Siganus rivulatus*. *J. World Aquac. Soc.* 41, 834–839. <https://doi.org/10.1111/j.1749-7345.2010.00427.x>
- Gines, R., Afonso, J.M., Arguello, A., Zamorano, M.J., Lopez, J.L., 2003. Growth in adult gilthead sea bream (*Sparus aurata* L) as a result of interference in sexual maturation by different photoperiod regimes. *Aquac. Res.* 34, 73–83. <https://doi.org/10.1046/j.1365-2109.2003.00801.x>

- Gonzalez, R.J., McDonald, D.G., 1992. the relationship between oxygen consumption and ion loss in a freshwater fish. *J. Exp. Biol.* 163.
- Good, C., Davidson, J., 2016. A Review of Factors Influencing Maturation of Atlantic Salmon, *Salmo salar* , with Focus on Water Recirculation Aquaculture System Environments. *J. World Aquac. Soc.* 47, 605–632. <https://doi.org/10.1111/jwas.12342>
- Graziano, M., Benito, R., Planas, J. V., Palstra, A.P., 2018. Swimming exercise to control precocious maturation in male seabass (*Dicentrarchus labrax*). *BMC Dev. Biol.* 18, 10. <https://doi.org/10.1186/s12861-018-0170-8>
- Hammer, C., 1995. Fatigue and exercise tests with fish. *Comp. Biochem. Physiol. Part A Physiol.* 112, 1–20. [https://doi.org/10.1016/0300-9629\(95\)00060-K](https://doi.org/10.1016/0300-9629(95)00060-K)
- Hay, J.B., Andrade, W.N., 1998. Lymphocyte recirculation, exercise, and immune responses. *Can. J. Physiol. Pharmacol.* 76, 490–496. <https://doi.org/10.1139/y98-051>
- Houlihan, D.F., Laurent, P., 1987. Effects of Exercise Training on the Performance, Growth, and Protein Turnover of Rainbow Trout (*Salmo gairdneri*). *Can. J. Fish. Aquat. Sci.* 44, 1614–1621. <https://doi.org/10.1139/f87-195>
- Huntingford, F., Kadri, S., 2013. Exercise, Stress and Welfare, in: Palstra, A., Planas, J. (Eds.), *Swimming Physiology of Fish*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 161–174. https://doi.org/10.1007/978-3-642-31049-2_7
- Huntingford, F.A., Adams, C., Braithwaite, V.A., Kadri, S., Pottinger, T.G., Sandoe, P., Turnbull, J.F., 2006. Current issues in fish welfare. *J. Fish Biol.* 68, 332–372. <https://doi.org/10.1111/j.0022-1112.2006.001046.x>
- Hurley, S.M., Schom, C.B., 1984. Genetic control of swimming stamina in Atlantic salmon (*Salmo salar*). *Can. J. Genet. Cytol.* 26, 57–61. <https://doi.org/10.1139/g84-010>
- Ibarz, A., Felip, O., Fernández-Borràs, J., Martín-Pérez, M., Blasco, J., Torrella, J.R., 2011. Sustained swimming improves muscle growth and cellularity in gilthead sea bream. *J. Comp. Physiol. B* 181, 209–217. <https://doi.org/10.1007/s00360-010-0516-4>
- Jobling, M., 2002. Environmental Factors and Rates of Development and Growth, in: Hart, P.J.B., Reynolds, J.D. (Eds.), *Handbook of Fish Biology and Fisheries*, Volume 1. Blackwell Publishing Ltd, Oxford, pp. 97–122. <https://doi.org/10.1002/9780470693803.ch5>
- Jobling, M., Baardvik, B., Christiansen, J., Jorgensen, E., 1993. The effects of prolonged exercise training on growth performance and production parameters in fish. *Aquac. Int.*

1, 95–111.

- Jonsson, B., Jonsson, N., 2009. Restoration and Enhancement of Salmonid Populations and Habitats with Special Reference to Atlantic Salmon, in: Haro, A., Avery, T., Beal, K. (Eds.), *Challenges for Diadromous Fishes in a Dynamic Global Environment*, American Fisheries Society Symposium. pp. 497–535.
- Jørgensen, E.H., Baardvik, B.M., Eliassen, R., Jobling, M., 1996. Food acquisition and growth of juvenile Atlantic salmon (*Salmo salar*) in relation to spatial distribution of food. *Aquaculture* 143, 277–289. [https://doi.org/10.1016/0044-8486\(96\)01287-2](https://doi.org/10.1016/0044-8486(96)01287-2)
- Jørgensen, E.H., Christiansen, J.S., Jobling, M., 1993. Effects of stocking density on food intake, growth performance and oxygen consumption in Arctic charr (*Salvelinus alpinus*). *Aquaculture* 110, 191–204. [https://doi.org/10.1016/0044-8486\(93\)90272-Z](https://doi.org/10.1016/0044-8486(93)90272-Z)
- Jørgensen, E.H., Jobling, M., 1993. The effects of exercise on growth, food utilisation and osmoregulatory capacity of juvenile Atlantic salmon, *Salmo salar*. *Aquaculture* 116, 233–246. [https://doi.org/10.1016/0044-8486\(93\)90011-M](https://doi.org/10.1016/0044-8486(93)90011-M)
- Karlsen, O., Norberg, B., Kjesbu, O., Taranger, G., 2006. Effects of photoperiod and exercise on growth, liver size, and age at puberty in farmed Atlantic cod (*Gadus morhua* L.). *ICES J. Mar. Sci.* 63, 355–364. <https://doi.org/10.1016/j.icesjms.2005.10.013>
- Kaufmann, R., 1990. Respiratory Cost of Swimming in Larval and Juvenile Cyprinids. *J. Exp. Biol.* 150.
- Khan, J.R., Trembath, C., Pether, S., Bruce, M., Walker, S.P., Herbert, N.A., 2014. Accommodating the cost of growth and swimming in fish—the applicability of exercise-induced growth to juvenile hapuku (*Polyprion oxygeneios*). *Front. Physiol.* 5, 448. <https://doi.org/10.3389/fphys.2014.00448>
- Kieffer, J., Alsop, D., Wood, C., 1998. A respirometric analysis of fuel use during aerobic swimming at different temperatures in rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* 201, 3123–3133.
- Kieffer, J.D., Kassie, R.S., Taylor, S.G., 2011. The effects of low-speed swimming following exhaustive exercise on metabolic recovery and swimming performance in brook trout (*Salvelinus fontinalis*). *Physiol. Biochem. Zool.* 84, 385–393. <https://doi.org/10.1086/660891>
- Kiessling, A., Higgs, D.A., Dosanjh, B.S., Eales, J.G., 1994. Influence of Sustained Exercise at Two Ration Levels on Growth and Thyroid Function of All-Female Chinook Salmon (

- Oncorhynchus tshawytscha*) in Seawater. *Can. J. Fish. Aquat. Sci.* 51, 1975–1984.
<https://doi.org/10.1139/f94-200>
- Kiessling, A., Pickova, J., Eales, J.G., Dosanjh, B., Higgs, D., 2005. Age, ration level, and exercise affect the fatty acid profile of chinook salmon (*Oncorhynchus tshawytscha*) muscle differently. *Aquaculture* 243, 345–356.
<https://doi.org/10.1016/J.AQUACULTURE.2004.10.003>
- Lackner, R., Weisler, W., Huber, M., Dalla Via, J., 1988. Responses of the intermediary metabolism to acute handling stress and recovery in untrained and trained *Leuciscus Cephalus* (Cyprinidae, Teleostei). *J. Exp. Biol.* 140, 393–404.
- Larsen, B.K., Skov, P. V., McKenzie, D.J., Jokumsen, A., 2012. The effects of stocking density and low level sustained exercise on the energetic efficiency of rainbow trout (*Oncorhynchus mykiss*) reared at 19°C. *Aquaculture* 324–325, 226–233.
<https://doi.org/10.1016/j.aquaculture.2011.10.021>
- Lauff, R.F., Wood, C.M., 1997. Effects of training on respiratory gas exchange, nitrogenous waste excretion, and fuel usage during aerobic swimming in juvenile rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* 54, 566–571.
- Lee, C.G., Farrell, A.P., Lotto, A., MacNutt, M.J., Hinch, S.G., Healey, M.C., 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, 3239–3251. <https://doi.org/10.1242/jeb.00547>
- Leon, K.A., 1986. Effect of Exercise on Feed Consumption, Growth, Food Conversion, and Stamina of Brook Trout. *Progress. Fish-Culturist* 48, 43–46.
[https://doi.org/10.1577/1548-8640\(1986\)48<43:EOEOFC>2.0.CO;2](https://doi.org/10.1577/1548-8640(1986)48<43:EOEOFC>2.0.CO;2)
- Li, X.-M., Liu, L., Yuan, J.-M., Xiao, Y.-Y., Fu, S.-J., Zhang, Y.-G., 2016. The effect of aerobic exercise and starvation on growth performance and postprandial metabolic response in juvenile southern catfish (*Silurus meridionalis*). *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 193, 36–44. <https://doi.org/10.1016/J.CBPA.2016.01.007>
- Li, X.M., Yu, L.J., Wang, C., Zeng, L.Q., Cao, Z.D., Fu, S.J., Zhang, Y.G., 2013. The effect of aerobic exercise training on growth performance, digestive enzyme activities and postprandial metabolic response in juvenile qingbo (*Spinibarbus sinensis*). *Comp. Biochem. Physiol. - A Mol. Integr. Physiol.* 166, 8–16.
<https://doi.org/10.1016/j.cbpa.2013.04.021>

- Liew, H.J., Sinha, A.K., Mauro, N., Diricx, M., Blust, R., De Boeck, G., 2012. Fasting goldfish, *Carassius auratus*, and common carp, *Cyprinus carpio*, use different metabolic strategies when swimming. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 163, 327–335. <https://doi.org/10.1016/J.CBPA.2012.07.012>
- Liu, G., Wu, Y., Qin, X., Shi, X., Wang, X., 2018. The effect of aerobic exercise training on growth performance, innate immune response and disease resistance in juvenile *Schizothorax prenanti*. *Aquaculture* 486, 18–25. <https://doi.org/10.1016/J.AQUACULTURE.2017.12.006>
- Luchiani, A.C., Chacon, D.M.M., 2013. Physical exercise improves learning in zebrafish, *Danio rerio*. *Behav. Processes* 100, 44–47. <https://doi.org/10.1016/J.BEPROC.2013.07.020>
- Ma, C.-L., Ma, X.-T., Wang, J.-J., Liu, H., Chen, Y.-F., Yang, Y., 2017. Physical exercise induces hippocampal neurogenesis and prevents cognitive decline. *Behav. Brain Res.* 317, 332–339. <https://doi.org/10.1016/J.BBR.2016.09.067>
- Magnoni, L.J., Felip, O., Blasco, J., Planas, J. V., 2013. Metabolic Fuel Utilization During Swimming: Optimizing Nutritional Requirements for Enhanced Performance, in: *Swimming Physiology of Fish*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 203–235. https://doi.org/10.1007/978-3-642-31049-2_9
- Marras, S., Killen, S.S., Lindström, J., McKenzie, D.J., Steffensen, J.F., Domenici, P., 2015. Fish swimming in schools save energy regardless of their spatial position. *Behav. Ecol. Sociobiol.* 69, 19–226. <https://doi.org/10.1007/s00265-014-1834-4>
- McKenzie, D.J., 2011. Swimming and other activities | Energetics of Fish Swimming, *Encyclopedia of Fish Physiology*. Elsevier Inc. <https://doi.org/10.1016/B978-0-12-374553-8.00151-9>
- McKenzie, D.J., Höglund, E., Dupont-Prinet, a., Larsen, B.K., Skov, P.V., Pedersen, P.B., Jokumsen, a., 2012. Effects of stocking density and sustained aerobic exercise on growth, energetics and welfare of rainbow trout. *Aquaculture* 338–341, 216–222. <https://doi.org/10.1016/j.aquaculture.2012.01.020>
- McKenzie, D.J., Martinez, R., Morales, A., Acosta, J., Morales, R., Taylor, E.W., Steffensen, J.F., Estrada, M.P., 2003. Effects of growth hormone transgenesis on metabolic rate, exercise performance and hypoxia tolerance in tilapia hybrids. *J. Fish Biol.* 63, 398–409. <https://doi.org/10.1046/j.1095-8649.2003.00162.x>

- Mercier, C., Aubin, J., Lefrancois, C., Claireaux, G., 2000. Cardiac disorders in farmed adult brown trout, *Salmo trutta* L. *J. Fish Dis.* 23, 243–249. <https://doi.org/10.1046/j.1365-2761.2000.00237.x>
- Mes, D., Dirks, R.P., Palstra, A.P., 2016. Simulated migration under mimicked photothermal conditions enhances sexual maturation of farmed European eel (*Anguilla anguilla*). *Aquaculture* 452, 367–372. <https://doi.org/10.1016/J.AQUACULTURE.2015.11.020>
- Mes, D., Palstra, A., Henkel, C., Vindas, M., Mayer, I., 2018. Brain training: Can swimming exercise promote brain plasticity and cognitive performance in Atlantic salmon?, in: 13th International Congress on the Biology of Fish.
- Mes, D., Palstra, A.P., Henkel, C. V., Mayer, I., Vindas, M.A., 2020. Swimming exercise enhances brain plasticity in fish. *R. Soc. Open Sci.* 7, 191640. <https://doi.org/10.1098/rsos.191640>
- Meyer, W.F., Cook, P.A., 1996. An assessment of the use of low-level aerobic swimming in promoting recovery from handling stress in rainbow trout. *Aquac. Int.* 4, 169–174. <https://doi.org/10.1007/BF00140597>
- Milligan, C.L., Hooke, G.B., Johnson, C., 2000. Sustained swimming at low velocity following a bout of exhaustive exercise enhances metabolic recovery in rainbow trout. *J. Exp. Biol.* 203, 921–926. [https://doi.org/10.1016/0300-9629\(93\)90373-c](https://doi.org/10.1016/0300-9629(93)90373-c)
- Nestor, K., Noble, D., Zhu, N., Moritsu, Y., 1996. Direct and correlated responses to long-term selection for increased body weight and egg production in turkeys. *Poult. Sci.* 75, 1180–1191.
- Nicoletto, P.F., 1995. Offspring quality and female choice in the guppy, *Poecilia reticulata*. *Anim. Behav.* 49, 377–387. <https://doi.org/10.1006/ANBE.1995.0050>
- Ogata, H.Y., Oku, H., 2000. Effects of Water Velocity on Growth Performance of Juvenile Japanese Flounder *Paralichthys olivaceus*. *J. World Aquac. Soc.* 31, 225–231. <https://doi.org/10.1111/j.1749-7345.2000.tb00357.x>
- Ohlberger, J., Staaks, G., Hölker, F., 2006. Swimming efficiency and the influence of morphology on swimming costs in fishes. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* 176, 17–25. <https://doi.org/10.1007/s00360-005-0024-0>
- Palstra, A.P., Crespo, D., van den Thillart, G.E.E.J.M., Planas, J. V., 2010a. Saving energy to fuel exercise: swimming suppresses oocyte development and downregulates ovarian transcriptomic response of rainbow trout *Oncorhynchus mykiss*. *Am. J. Physiol. Integr.*

- Comp. Physiol. 299, R486–R499. <https://doi.org/10.1152/ajpregu.00109.2010>
- Palstra, A.P., Mes, D., Kusters, K., Roques, J.A.C., Flik, G., Kloet, K., Blonk, R.J.W., 2015. Forced sustained swimming exercise at optimal speed enhances growth of juvenile yellowtail kingfish (*Seriola lalandi*). *Front. Physiol.* 5, 506. <https://doi.org/10.3389/fphys.2014.00506>
- Palstra, A.P., Planas, J. V., 2013. Swimming physiology of fish: Towards using exercise to farm a fit fish in sustainable aquaculture, *Swimming Physiology of Fish: Towards Using Exercise to Farm a Fit Fish in Sustainable Aquaculture*. Springer Berlin Heidelberg. <https://doi.org/10.1007/978-3-642-31049-2>
- Palstra, A.P., Tudorache, C., Rovira, M., Brittijn, S.A., Burgerhout, E., van den Thillart, G.E.E.J.M., Spaink, H.P., Planas, J. V., 2010b. Establishing zebrafish as a novel exercise model: Swimming economy, swimming-enhanced growth and muscle growth marker gene expression. *PLoS One* 5. <https://doi.org/10.1371/journal.pone.0014483>
- Palstra, A.P., van den Thillart, G.E.E.J.M., 2010. Swimming physiology of European silver eels (*Anguilla anguilla* L.): energetic costs and effects on sexual maturation and reproduction. *Fish Physiol. Biochem.* 36, 297–322. <https://doi.org/10.1007/s10695-010-9397-4>
- Pascoe, A.R., Fiatarone Singh, M.A., Edwards, K.M., 2014. The effects of exercise on vaccination responses: A review of chronic and acute exercise interventions in humans. *Brain. Behav. Immun.* 39, 33–41. <https://doi.org/10.1016/J.BBI.2013.10.003>
- Peters, C.J., 2009. Continuous Exercise Enhances Swim Performance and Alters Growth Rate, IGF-I, and Cortisol in Juvenile Marine Finfish in Aquaculture. University of San Diego, MSc Thesis.
- Pettersson, L.B., Hedenström, A., 2000. Energetics, cost reduction and functional consequences of fish morphology. *Proc. R. Soc. London. Ser. B Biol. Sci.* 267, 759–764. <https://doi.org/10.1098/rspb.2000.1068>
- Poppe, T.T., Taksdal, T., Bergtun, P.H., 2007. Suspected myocardial necrosis in farmed Atlantic salmon, *Salmo salar* L.: a field case. *J. Fish Dis.* 30, 615–620. <https://doi.org/10.1111/j.1365-2761.2007.00841.x>
- Randall, D.J., Baumgarten, D., Malyusz, M., 1972. The relationship between gas and ion transfer across the gills of fishes. *Comp. Biochem. Physiol. Part A Physiol.* 41, 629–637. [https://doi.org/10.1016/0300-9629\(72\)90017-5](https://doi.org/10.1016/0300-9629(72)90017-5)

- Rasmussen, R.S., Heinrich, M.T., Hyldig, G., Jacobsen, C., Jokumsen, A., 2011. Moderate exercise of rainbow trout induces only minor differences in fatty acid profile, texture, white muscle fibres and proximate chemical composition of fillets. *Aquaculture* 314, 159–164. <https://doi.org/10.1016/J.AQUACULTURE.2011.02.003>
- Rauw, W., Kanis, E., Noordhuizen-Stassen, E., Grommers, F., 1998. Undesirable side effects of selection for high production efficiency in farm animals: a review. *Livest. Prod. Sci.* 56, 15–33. [https://doi.org/10.1016/S0301-6226\(98\)00147-X](https://doi.org/10.1016/S0301-6226(98)00147-X)
- Richards, J.G., Mercado, A.J., Clayton, C. a, Heigenhauser, G.J.F., Wood, C.M., 2002. Substrate utilization during graded aerobic exercise in rainbow trout. *J. Exp. Biol.* 205, 2067–77.
- Robinson, N.A., Timmerhaus, G., Baranski, M., Andersen, Ø., Takle, H., Krasnov, A., 2017. Training the salmon’s genes: influence of aerobic exercise, swimming performance and selection on gene expression in Atlantic salmon. *BMC Genomics* 18, 971. <https://doi.org/10.1186/s12864-017-4361-7>
- Rodnick, K.J., Planas, J. V., 2016. *The Stress and Stress Mitigation Effects of Exercise: Cardiovascular, Metabolic, and Skeletal Muscle Adjustments*. Elsevier Inc. <https://doi.org/10.1016/B978-0-12-802728-8.00007-2>
- Rovira, M., Arrey, G., Planas, J. V., 2017. Exercise-Induced Hypertrophic and Oxidative Signaling Pathways and Myokine Expression in Fast Muscle of Adult Zebrafish. *Front. Physiol.* 8, 1063. <https://doi.org/10.3389/fphys.2017.01063>
- Sánchez-Gurmaches, J., Cruz-García, L., Ibarz, A., Fernández-Borrás, J., Blasco, J., Gutiérrez, J., Navarro, I., 2013. Insulin, IGF-I, and muscle MAPK pathway responses after sustained exercise and their contribution to growth and lipid metabolism regulation in gilthead sea bream. *Domest. Anim. Endocrinol.* 45, 145–153. <https://doi.org/10.1016/J.DOMANIEND.2013.08.001>
- Schreck, C.B., Tort, L., 2016. *The Concept of Stress in Fish*, First Edit. ed, *Fish Physiology*. Elsevier Inc. <https://doi.org/10.1016/B978-0-12-802728-8.00001-1>
- Schulte, P.M., 2014. What is environmental stress? Insights from fish living in a variable environment. *J. Exp. Biol.* 217, 23–34. <https://doi.org/10.1242/jeb.089722>
- Shrivastava, J., Rašković, B., Blust, R., De Boeck, G., 2018. Exercise improves growth, alters physiological performance and gene expression in common carp (*Cyprinus carpio*). *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 226, 38–48.

<https://doi.org/10.1016/J.CBPA.2018.08.007>

Skov, P.V., Larsen, B.K., Frisk, M., Jokumsen, A., 2011. Effects of rearing density and water current on the respiratory physiology and haematology in rainbow trout, *Oncorhynchus mykiss* at high temperature. *Aquaculture* 319, 446–452.

<https://doi.org/10.1016/J.AQUACULTURE.2011.07.008>

Skov, P. V., Lund, I., Pargana, A.M., 2015. No evidence for a bioenergetic advantage from forced swimming in rainbow trout under a restrictive feeding regime. *Front. Physiol.* 6, 31. <https://doi.org/10.3389/fphys.2015.00031>

Soya, H., Nakamura, T., Deocaris, C.C., Kimpara, A., Iimura, M., Fujikawa, T., Chang, H., McEwen, B.S., Nishijima, T., 2007. BDNF induction with mild exercise in the rat hippocampus. *Biochem. Biophys. Res. Commun.* 358, 961–967.

<https://doi.org/10.1016/J.BBRC.2007.04.173>

Steffensen, J.F., 1985. The Transition between Branchial Pumping and Ram Ventilation in Fishes: Energetic Consequences and Dependence on Water Oxygen Tension. *J. Exp. Biol.* 114.

Steinhausen, M.F., Fleng Steffensen, J., Gerner Andersen, N., 2010. The effects of swimming pattern on the energy use of gilthead seabream (*Sparus aurata* L.). *Mar. Freshw. Behav. Physiol.* 43, 227–241. <https://doi.org/10.1080/10236244.2010.501135>

Suski, C.D., Cooke, S.J., Tufts, B.L., 2015. Failure of low-velocity swimming to enhance recovery from exhaustive exercise in largemouth bass (*Micropterus salmoides*). *Physiol. Biochem. Zool.* 80, 78–87. <https://doi.org/10.1086/509058>

Taranger, G., Aardal, L., Hansen, T., Kjesbu, O., 2006. Continuous light delays sexual maturation and increases growth of Atlantic cod (*Gadus morhua* L.) in sea cages. *ICES J. Mar. Sci.* 63, 365–375. <https://doi.org/10.1016/j.icesjms.2005.10.014>

Thorstad, E.B., Uglem, I., Arechavala-Lopez, P., Økland, F., Finstad, B., 2011. Low survival of hatchery-released Atlantic salmon smolts during initial river and fjord migration. *Boreal Environ. Res.* 16, 115–120.

Totland, G.K., Kryvi, H., Jødestøl, K.A., Christiansen, E.N., Tangerås, A., Slinde, E., 1987. Growth and composition of the swimming muscle of adult Atlantic salmon (*Salmo salar* L.) during long-term sustained swimming. *Aquaculture* 66, 299–313.

[https://doi.org/10.1016/0044-8486\(87\)90115-3](https://doi.org/10.1016/0044-8486(87)90115-3)

Tsatsoulis, A., Fountoulakis, S., 2006. The protective role of exercise on stress system

- dysregulation and comorbidities. *Ann. N. Y. Acad. Sci.* 1083, 196–213.
<https://doi.org/10.1196/annals.1367.020>
- Tucker, V.A., 1970. Energetic cost of locomotion in animals. *Comp. Biochem. Physiol.* 34, 841–846.
- Tudorache, C., O’Keefe, R.A., Benfey, T.J., 2011. Optimal swimming speeds reflect preferred swimming speeds of brook charr (*Salvelinus fontinalis* Mitchill, 1874). *Fish Physiol. Biochem.* 37, 307–315. <https://doi.org/10.1007/s10695-011-9498-8>
- van Praag, H., 2008. Neurogenesis and Exercise: Past and Future Directions. *NeuroMolecular Med.* 10, 128–140. <https://doi.org/10.1007/s12017-008-8028-z>
- Vandeputte, M., Porte, J.D., Auferin, B., Dupont-Nivet, M., Vergnet, A., Valotaire, C., Claireaux, G., Prunet, P., Chatain, B., 2016. Quantitative genetic variation for post-stress cortisol and swimming performance in growth-selected and control populations of European sea bass (*Dicentrarchus labrax*). *Aquaculture* 455, 1–7.
<https://doi.org/10.1016/J.AQUACULTURE.2016.01.003>
- Vaynman, S., Ying, Z., Gomez-Pinilla, F., 2004. Hippocampal BDNF mediates the efficacy of exercise on synaptic plasticity and cognition. *Eur. J. Neurosci.* 20, 2580–2590.
<https://doi.org/10.1111/j.1460-9568.2004.03720.x>
- Veiseth, E., Fjaera, S.O., Bjerkeng, B., Skjervold, P.O., 2006. Accelerated recovery of Atlantic salmon (*Salmo salar*) from effects of crowding by swimming. *Comp. Biochem. Physiol. B. Biochem. Mol. Biol.* 144, 351–8. <https://doi.org/10.1016/j.cbpb.2006.03.009>
- Videler, J.J., 1993. *Fish Swimming*. Chapman and Hall, London.
- Waldrop, T., Summerfelt, S., Mazik, P., Good, C., 2018. The effects of swimming exercise and dissolved oxygen on growth performance, fin condition and precocious maturation of early-rearing Atlantic salmon *Salmo salar*. *Aquac. Res.* 49, 801–808.
<https://doi.org/10.1111/are.13511>
- Webb, P.W., 1998. Swimming, in: Evans, D.D. (Ed.), *The Physiology of Fishes*. CRC Press, Boca Raton, pp. 1–38.
- Weihs, D., Keyes, R.S., Stalls, D.M., 1981. Voluntary Swimming Speeds of Two Species of Large Carcharhinid Sharks. *Copeia* 1981, 219. <https://doi.org/10.2307/1444062>
- Wilson, R.O.D.W., Egginton, S., 1994. Assessment of maximum sustainable swimming performance in rainbow trout (*Oncorhynchus mykiss*) 305, 299–305.
- Woodward, J., Smith, L., 1985. Exercise training and the stress response in rainbow trout,

- Salmo gairdneri* Richardson. J. Fish Biol. 26, 435–447.
- Yogata, H., Oku, H., 2000. The effects of swimming exercise on growth and whole-body protein and fat contents of fed and unfed fingerling yellowtail. Fish. Sci. 66, 1100–1105.
- Young, P.S., Cech Jr., J.J., 1993. Effects of Exercise Conditioning on Stress Responses and Recovery in Cultured and Wild Young-of-the-Year Striped Bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 50, 2094–2099. <https://doi.org/10.1139/f93-233>
- Zupanc, G.K.H., 2006. Neurogenesis and neuronal regeneration in the adult fish brain. J. Comp. Physiol. A 192, 649–670. <https://doi.org/10.1007/s00359-006-0104-y>
- Zupanc, G.K.H., Sîrbulescu, R.F., 2011. Adult neurogenesis and neuronal regeneration in the central nervous system of teleost fish. Eur. J. Neurosci. 34, 917–929. <https://doi.org/10.1111/j.1460-9568.2011.07854.x>

Table 1. Studies that have investigate the effects of forced aerobic swimming on growth performance in non-salmonid finfish species. The table carries information about initial body mass (BM), initial forklength (L_I , when reported), swim speed (U), fish per tank (Tank), Temperature (T), feed intake (FI, when reported); feeding protocol (FP), feed conversion (FCR, when reported), specific growth rate (SGR), and the associated literature reference. R

Species	Order, Family	BM _I (g)	BM _F (g)	L_I (mm)	U (BL s ⁻¹)	Tank	T (°C)	FI (g day ⁻¹)	FP	FCR	SGR (g day ⁻¹)	Reference
Perciformes												
<i>Sparus aurata</i>	Sparidae	88±1	98±2		0	200C	20	2.6	AL		0.61	(Ibarz et al., 2011)
		90±1	107±2		1.5	400C	20	2.8	AL		0.76	
		5.0±0.1	14.5±0.5		0	200C	23		AL	1.17	3.41	(Blasco et al., 2015)
		5.1±0.2	20.3±0.4		5	400C	23		AL	0.93	3.72	
		50-60	70±2		0	200C	22	3.56±0.20	AL		1.13±0.05	(Felip et al., 2012)
		50-60	74±2		1.5	400C	22	3.84±0.03	AL		1.32±0.06	
<i>Pagrus major</i>	Sparidae	2.5±0.5	13.8		0	35C	27.5	3.16	AL ×2	0.81	4.4	(Forster and Ogata, 1996)
		2.5±0.5	13.8		1.5	35C	27.5	3.16	AL ×2	0.83	4.5	
		2.5±0.5	12.7		3.0	35C	27.5	2.92	AL ×2	0.79	4.2	
		2.5±0.5	14.7		0	35C	27.5	3.25	AL ×2	0.81	4.6	
		2.5±0.5	15.2		1.5	35C	27.5	3.03	AL ×2	0.75	4.6	
		2.5±0.5	12.2		3.0	35C	27.5	3.40	AL ×2	0.94	4.1	

		18±1	27.3		0	35C	25	2.5	RE	1.27	1.56	
		18±1	25.8		1	35C	25	2.5	RE	1.43	1.39	
		18±1	26.7		2	35C	25	2.5	RE	1.47	1.42	
		18±1	27.5		0	35C	25	2.5	RE	1.20	1.62	
		18±1	27.0		1	35C	25	2.5	RE	1.39	1.44	
		18±1	26.4		2	35C	25	2.5	RE	1.45	1.37	
<i>Seriola</i>												(Yogata and
<i>quinqueradi</i>												Oku, 2000)
<i>ata</i>	Carangidae	4.3±0.1	22.8±0.8	73	0.3	40C	23	4.44	AL ×2	0.71	6.03	
		4.3±0.1	30.5±1.7	73	1.0	40C	23	4.30	AL ×2	0.63	7.00	
		4.4±0.02	30.5±1.1	73	2.25	40C	23	4.21	AL ×2	0.62	6.94	
		4.4±0.1	25.1±0.9	74	0.3	40C	23	4.36	AL ×2	0.68	6.23	
		4.3±0.1	29.9±0.7	73	1.0	40C	23	4.27	AL ×2	0.62	6.92	
<i>Seriola</i>												(Palstra et al.,
<i>lalandi</i>	Carangidae	504±27	661±32	346	0.0	3600F	23.6	2.65	RE ×2	1.77	1.5	2015)
		504±27	735±23	346	2.46	3600F	23.6	2.65	RE ×2	1.21	2.1	
<i>Seriola</i>												(Brown et al.,
<i>lalandi</i>	Carangidae	1591±7		476	0.0	13000C	14.9		AL ×2	2.39	0.42	2011)
		1591±7		476	0.75	13000C	14.9		AL ×2	2.18	0.4	
		179±5		236	0.0	1000C	21.1		AL ×2	2.05	0.8	
		179±5		236	0.75	1000C	21.1		AL ×2	1.89	0.88	
		179±5		236	1.54	1000C	21.1		AL ×2	1.93	0.86	
		179±5		236	2.25	1000C	21.1		AL ×2	1.98	0.82	
<i>Siganus</i>												(Ghanawi et
<i>rivulatus</i>	Siganidae	7.0±0.2	15.4±0.5	89	0.0	1000C	26	3.0	RE ×2	1.3	2.13	al., 2010)

		7.6±0.2	13.7±0.4	91	1.5	1000C	26	3.0	RE ×2	1.8	1.6	
<i>Polyprion</i>												(Khan et al.,
<i>oxygeneios</i>	Polyprionidae	120±3	341±10		0.0	1600C	17	218*	AL ×2	0.97	1.81	2014)
		131±5	367±10		0.25	1600C	17	227*	AL ×2	0.97	1.85	
		129±5	381±13		0.5	1600C	17	236*	AL ×2	0.97	1.88	
		123±5	365±12		0.75	1600C	17	243*	AL ×2	0.99	1.88	
		133±4	376±7		1.0	1600C	17	249*	AL ×2	1.01	1.86	
		139±3	381±8		1.5	1600C	17	258*	AL ×2	1.07	1.77	
		170±6	383±12		0.0	1600C	17	210*	AL ×2	1.01	1.40	
		170±8	373±6		0.25	1600C	17	220*	AL ×2	1.01	1.43	
		171±6	397±14		0.5	1600C	17	227*	AL ×2	1.01	1.44	
		187±11	424±20		0.75	1600C	17	230*	AL ×2	1.02	1.45	
		172±10	388±19		1.0	1600C	17	229*	AL ×2	1.03	1.44	
		167±6	372±6.		1.5	1600C	17	218*	AL ×2	1.07	1.40	
<hr/>												
	Gadiformes											
<i>Gadus</i>												(Karlsen et al.,
<i>morhua</i>	Gadidae	551	2200		0.5 -1.0	7000C	7		AL ×2			2006)
		450	2300		0.5 - 1.0	7000C	10		AL ×2			
<hr/>												
	Pleuronectiformes											
	s											
<i>Paralichthys</i>												(Ogata and
<i>olicaceus</i>	Paralichthyidae	5.7 ± 0.1	41.5 ± 1.3	91	0.3	35C	21	1.71	AL ×2	0.64	3.35	Oku, 2000)
		5.8 ± 0.1	44.8 ± 1.0	92	0.9	35C	21	1.75	AL ×2	0.64	3.45	
		5.7 ± 0.0	37.7 ± 1.3	91	2.1	35C	21	1.72	AL ×2	0.68	3.14	
<hr/>												
	Siluriformes											

<i>Silurus</i>											(Li et al.,
<i>meridionalis</i>	Siluridae	12.2±0.1	37.1±1.2	0	42F	25	5.8	AL ×1	2.09±0.12	2016)	
		12.0±0.1	35.7±0.9	1	42F	25	6.0	AL ×1	3.11	2.12±0.06	
		12.2±0.1	34.7±1.1	2	42F	25	6.4	AL ×1	3.46	2.01±0.06	
<hr/>											
	Cypriniformes										
<i>Schizothorax</i>											(Liu et al.,
<i>prenanti</i>	Cyprinidae	13.8±0.1	24.4±1.4	0	1200F		17.3±1.7*	AL ×2	1.64	0.95±0.08	2018)
		13.8±0.2	29.7±1.4	1	1200F		23.0±1.0*	AL ×2	1.45	1.28±0.07	
		13.8±0.2	31.2±1.4	2	1200F		24.3±1.2*	AL ×2	1.45	1.36±0.05	
		13.8±0.2	26.4±1.0	4	1200F		26.5±1.1*	AL ×2	2.13	1.08±0.05	
<i>Spinibarbus</i>											(Li et al., 2013)
<i>sinensis</i>	Cyprinidae	19.4±0.1	40.8±0.8	102	0	42F	25	1.63±0.03	AL ×2	1.29	1.32
		19.4±0.1	49.4±2.2	102	1	42F	25	1.94±0.05	AL ×2	1.25	1.66
		19.6±0.1	53.3±3.4	103	2	42F	25	2.05±0.04	AL ×2	1.25	1.79
		19.6±0.1	47.4±2.0	103	3	42F	25	2.22±0.01	AL ×2	1.50	1.58

BL, bodylength s⁻¹; C, circular; F, flume; AL, *ad-libitum*; RE, restricted; FCR calculated as feed mass/body mass gain.

Table 2. Studies that have investigated effects of chronic (days to months) sustained swimming exercise on circulating levels of cortisol in fishes.

Species	Mass (g)	Forklength (mm)	Current speed (BL s ⁻¹)	Density (kg m ⁻³)	Duration (days)	Plasma cortisol (ng ml ⁻¹)	Reference
Decreased plasma cortisol							
<i>Oncorhynchus mykiss</i>	28	120	0.0	43	30	83	(Woodward and Smith, 1985)
	29		1.5	43		41*	
<i>Salmo salar</i>	20	130	0.0	1.7	4		(Boesgaard et al., 1993)
			0.5				
<i>Morone saxatilis</i>	23		0.0	5-6	60	27	(Young and Cech Jr., 1993)
	26		0.5-1.2	5-6		19	
	27		1.5-2.4	5-6		3*	
	26		2.4-3.6	5-6		13	
<i>Brycon amazonicus</i>	18	120	0.0	1.63	70		(Arbeláez-Rojas et al., 2013)
				3.26			
				6.53			
			1.0	1.63			
				3.26			
				6.53			

No effect on plasma cortisol							
<i>O. mykiss</i>	242		0.0	25	60	1	(McKenzie et al., 2012)
	236		0.9			1	
	223		0.0	100		<1	
	224		0.9			<1	
<i>Atractoscion nobilis</i>	42	108	0.0	6.9	42		(Peters, 2009)
			1.3				
			2.0				
<i>Seriola lalandi</i>	34	84	0.0	7.6	34		(Peters, 2009)
			1.4				
			2.1				
Increased plasma cortisol							
<i>Salvelinus alpinus</i>	102	196	0.0	17-19	76	24	(Christiansen et al., 1991)
	106	198	1.3			40*	

Figure legends

Figure 1. a) Schematic picture showing different components of metabolic rate in fishes as swimming speed increases up to U_{ms} (maximum sustained swimming speed). The standard metabolic rate (SMR, the basal metabolic rate of ectothermic species at their acclimation temperature), is assumed to be constant at all swimming velocities. The cost of swimming increases exponentially with swimming velocity and the curve is derived from Webb (1971). The specific dynamic action (SDA, the metabolic cost of digesting and assimilating a meal) is assumed to be maintained at all swimming velocities (Alsop & Wood, 1997; Thorarensen & Farrell, 2006). b) The Cost of Transportation (COT, the energy consumed while swimming one metre) is calculated based on the values in Fig 1a.

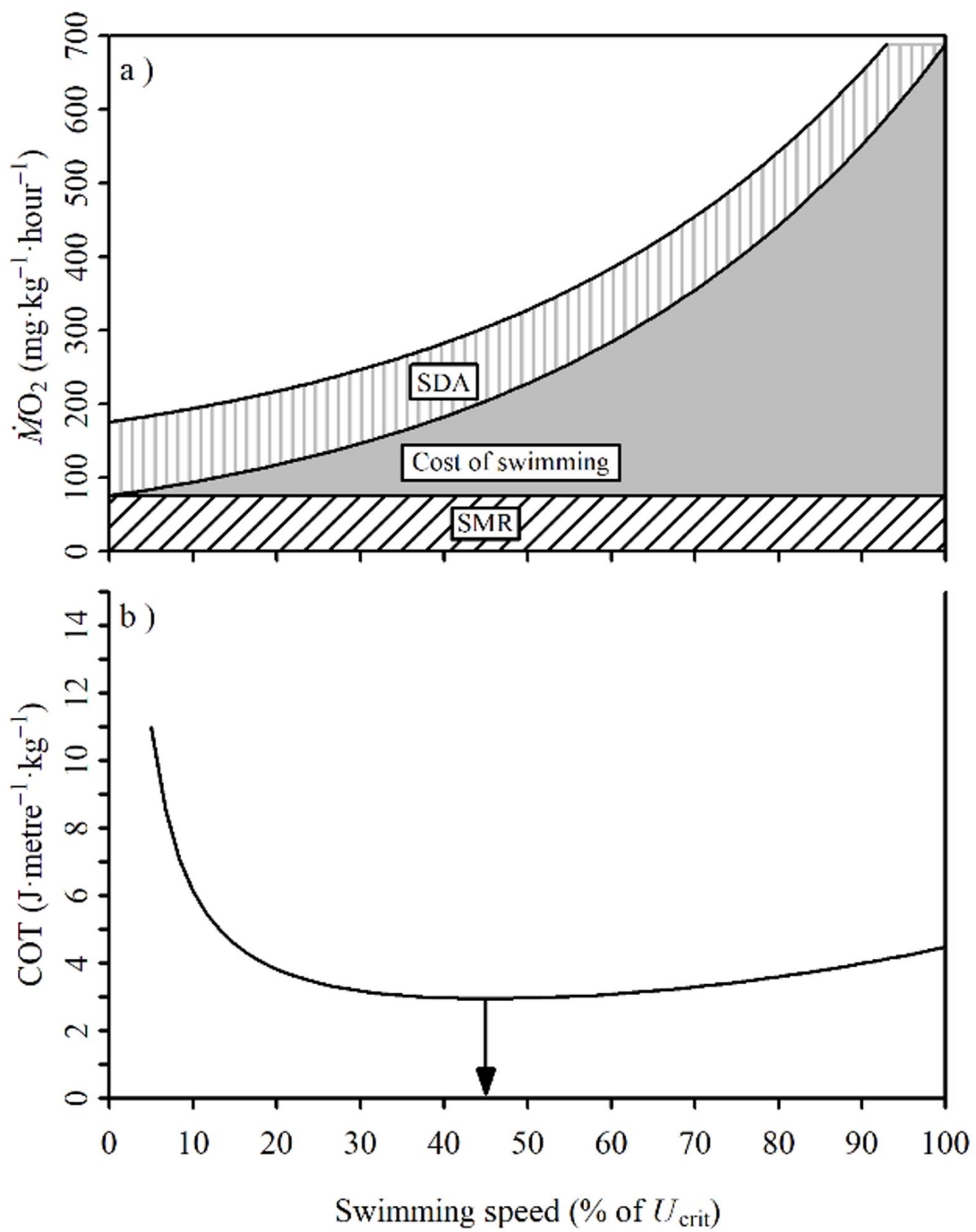


Figure 2. A conceptual model of the interplay among metabolic rate, feed intake and scope for growth in fish. At low velocities feed intake ① may or may not be reduced, and/or metabolic rate increased ②, due to increased levels of spontaneous activity or aggression. As a result, the scope for growth is reduced. If neither feed intake is reduced nor metabolic rate increased, scope for growth is maintained over different swimming velocities and there is no effect of swimming exercise on growth. At swimming velocities above 45-50% of the maximum sustained swimming speed (U_{ms}) growth is reduced because feed intake cannot meet the increased metabolic demands of swimming, and/or because feed intake is reduced ③.

