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

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27 **Abstract**

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

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 (Gallagher 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; Gallaughier 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.

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 983

984 **Table 1.** Studies that have investigate the effects of forced aerobic swimming on growth performance in non-salmonid finfish species. The
985 table carries information about initial body mass (BM), initial forklength (L_I, when reported), swim speed (U), fish per tank (Tank),
986 Temperature (T), feed intake (FI, when reported); feeding protocol (FP), feed conversion (FCR, when reported), specific growth rate
987 (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> <i>quinqueradi</i> <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	(Yogata and Oku, 2000)
		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> <i>lalandi</i>	Carangidae	504±27	661±32	346	0.0	3600F	23.6	2.65	RE ×2	1.77	1.5	(Palstra et al., 2015)
		504±27	735±23	346	2.46	3600F	23.6	2.65	RE ×2	1.21	2.1	
<i>Seriola</i> <i>lalandi</i>	Carangidae	1591±7		476	0.0	13000C	14.9		AL ×2	2.39	0.42	(Brown et al., 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> <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	(Ghanawi et 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

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

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990

991 Table 2. Studies that have investigated effects of chronic (days to months) sustained swimming exercise on circulating levels of cortisol in
 992 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 0.5	1.7	4		(Boesgaard et al., 1993)
<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			

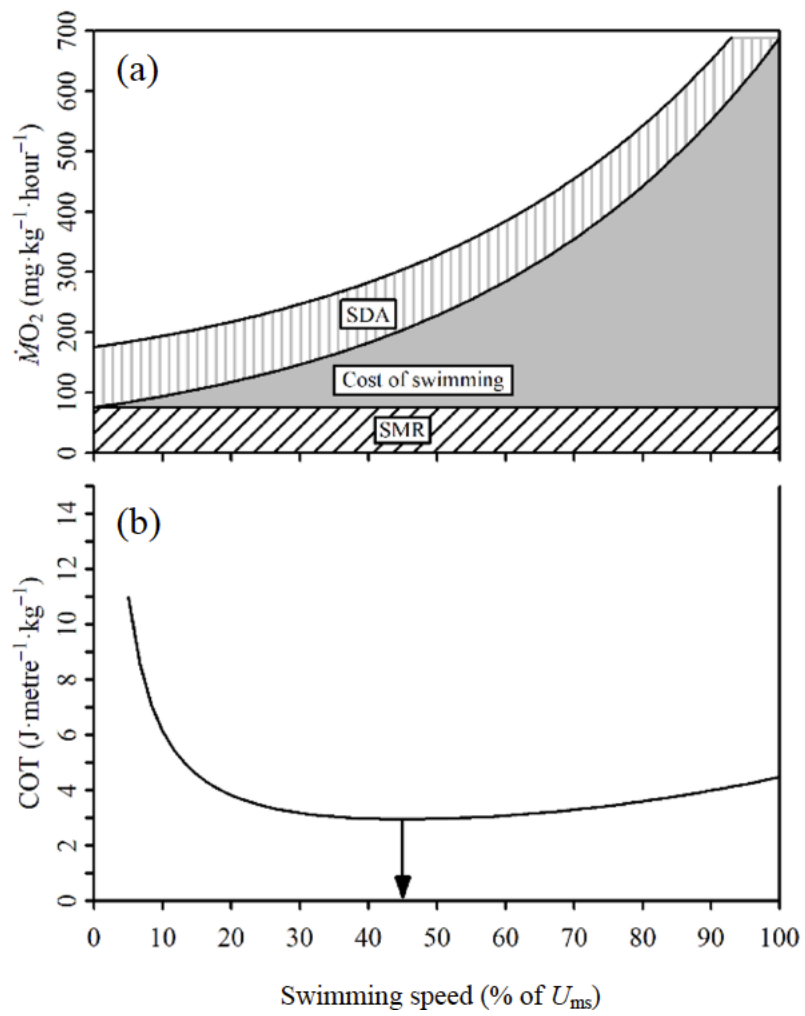
No effect on plasma cortisol						
<i>O. mykiss</i>	242		0.0	25	60	1 (McKenzie et al., 2012)
	236		0.9			1
	223		0.0	100		<1
	224		0.9			<1
<i>Atractoscion nobilis</i>	42	108	0.0	6.9	42	(Peters, 2009)
			1.3			
			2.0			
<i>Seriola lalandi</i>	34	84	0.0	7.6	34	(Peters, 2009)
			1.4			
			2.1			
Increased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

994 **Figure legends**

995 **Figure 1.** a) Schematic picture showing different components of metabolic rate in fishes as
996 swimming speed increases up to U_{ms} (maximum sustained swimming speed). The standard
997 metabolic rate (SMR, the basal metabolic rate of ectothermic species at their acclimation
998 temperature), is assumed to be constant at all swimming velocities. The cost of swimming
999 increases exponentially with swimming velocity and the curve is derived from Webb (1971).
1000 The specific dynamic action (SDA, the metabolic cost of digesting and assimilating a meal) is
1001 assumed to be maintained at all swimming velocities (Alsop & Wood, 1997; Thorarensen &
1002 Farrell, 2006). b) The Cost of Transportation (COT, the energy consumed while swimming
1003 one metre) is calculated based on the values in Fig 1a.

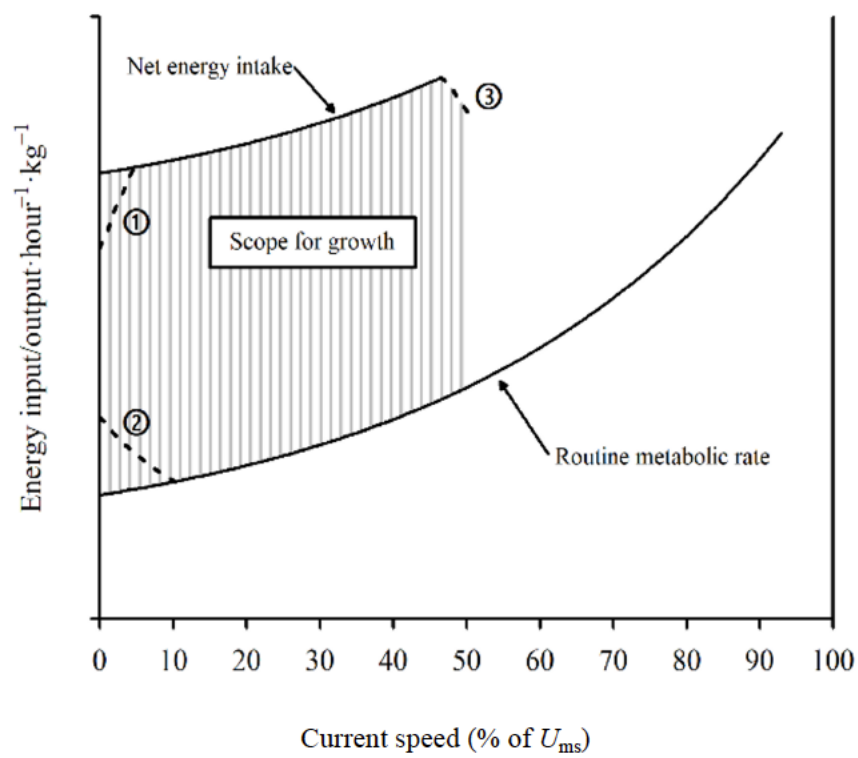
1004 **Figure 2.** A conceptual model of the interplay among metabolic rate, feed intake and scope
1005 for growth in fish. At low velocities feed intake ① may or may not be reduced, and/or
1006 metabolic rate increased ②, due to increased levels of spontaneous activity or aggression. As
1007 a result, the scope for growth is reduced. If neither feed intake is reduced nor metabolic rate
1008 increased, scope for growth is maintained over different swimming velocities and there is no
1009 effect of swimming exercise on growth. At swimming velocities above 45-50% of the
1010 maximum sustained swimming speed (U_{ms}) growth is reduced because feed intake cannot
1011 meet the increased metabolic demands of swimming, and/or because feed intake is reduced
1012 ③.

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