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

3

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26

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.

46 **Introduction**

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

54 With regard to production, sustained aerobic exercise has been reported to stimulate
55 growth and/or improve feed conversion for a variety of farmed species, under experimental
56 conditions (Davison and Herbert, 2013). This is of obvious potential interest, we review the
57 latest evidence and the potential underlying mechanisms, which range from animal behaviour
58 (Jørgensen and Jobling, 1993; Skov et al., 2011) to muscle cell biology (Ibarz et al., 2011). In
59 terms of mitigating the deleterious impacts of intensive aquaculture on the welfare of fishes,
60 exercise has been reported to alleviate chronic stress (Young and Cech, 1993) and to promote
61 recovery from acute stresses (McKenzie et al., 2012; Milligan et al., 2000). It may also
62 improve disease resistance (Castro et al., 2011), promote neuroplasticity and cognition (Mes
63 et al., 2020), and inhibit precocious sexual maturation (Graziano et al., 2018; Palstra et al.,
64 2010a). We review the evidence for these positive effects and their underlying mechanisms.
65 We briefly consider how observation of swimming behaviour may provide ‘operational
66 welfare indicators’ (OWI), especially in early life stages.

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

73 **Exercise and production: effects on growth**

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

78 such as muscle fibre sizes and densities (Davison and Goldspink, 1977; Rasmussen et al.,
79 2011), overall exercise performance capacity (Gallaughan et al., 2001), and the use of
80 metabolic fuels (Alsop and Wood, 1997; Richards et al., 2002). There was also a research
81 focus upon a more applied aspect, namely whether aerobic exercise could be used to improve
82 growth rates when farming fish species that, in nature, have an active lifestyle. This subject
83 has been extensively reviewed (Davison, 1997, 1989; Davison and Herbert, 2013; Jobling et
84 al., 1993) but new approaches and species continue to accrue, demanding a consideration of
85 current status and future directions. Although it is frequently reported that fishes submitted to
86 moderate swimming exercise have higher growth rates than those held in still water or at low
87 currents (e.g. Ibarz et al., 2011; Palstra et al., 2015; Shrivastava et al., 2018), other studies
88 have found that swimming exercise has no, or even negative, effects on growth (e.g. Kiessling
89 et al., 1994; McKenzie et al., 2012; Skov et al., 2015).

90 **Growth and energy balance**

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

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

108 **Energetic costs of aerobic swimming**

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

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

141 smallest of these factors (Fig. 1a). In addition, a need for stability control at low speeds may
142 also contribute to overall metabolic cost (Fitzgibbon et al., 2007). The cost of transport is
143 often specified as to whether or not it includes SMR, being either total cost of transport (T_{COT})
144 or net cost of transport (N_{COT}) respectively (Ohlberger et al., 2006); the latter is sometimes
145 also called the cost of swimming (COS, McKenzie et al., 2003). The T_{COT} typically shows a
146 'U-shape' against swimming speed, the elevated T_{COT} at low speeds (Fig. 1b) is primarily due
147 to the SMR occupying a large proportion of the total metabolic rate, with the cost of
148 swimming being low (Fig. 1a). The swimming speed at which the T_{COT} is the lowest has been
149 defined as the optimal swimming speed (U_{opt} , Fig 1b) (Tucker, 1970; Videler, 1993). It may be
150 important for fishes when they are foraging, where energy acquired can be proportional to the
151 distance travelled. The U_{opt} is influenced by environmental factors such as water temperature
152 (Claireaux et al., 2006) as well as by inherent characters of the fish, such as morphology, body
153 size, nutritional and reproductive status (Cai et al., 2014; Kaufmann, 1990; Pettersson and
154 Hedenström, 2000). In addition, schooling also reduces the cost of swimming (Marras et al.,
155 2015). There are reports that spontaneous preferred swimming speed of various species
156 coincides with their U_{opt} (e.g. Tudorache et al., 2011; Weihs et al., 1981). For farmed fishes,
157 food is supplied in abundance and access to feed is not directly proportional to the distance
158 covered. Thus, it could be argued that in an aquaculture context, any energy that is allocated
159 to aerobic swimming does not promote food acquisition and therefore does not contribute to
160 growth (Fig. 1a).

161 **What swimming speed to choose?**

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

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

179 **Fishes are active even when there is no current**

180 The swimming speed of fishes is not always determined by the water current. Even if kept in
181 still water, many species of fish will swim spontaneously and, under these conditions, their
182 metabolic rate may be increased (Fig 2) to the extent that it is either equal to (Christiansen et
183 al., 1991) or higher than that of fish swimming steadily against a moderate current (Skov et
184 al., 2011). In fact, swimming spontaneously with a complex turning trajectory can be
185 significantly more costly than swimming at the same speed but against a current and in a
186 straight line (Steinhausen et al., 2010). If not compensated for by increased energy intake, the
187 increased metabolic rate would reduce growth (Fig. 2). In still water or at very low swimming
188 speeds, increased activity levels of fishes can reflect increased levels of aggression, which
189 disappear when a current is provided that stimulates shoaling or schooling (Christiansen and
190 Jobling, 1990; Christiansen et al., 1989; East and Magnan, 1987; Jørgensen and Jobling,
191 1993). Aggression can result in reduced feed intake (Christiansen and Jobling, 1990;
192 Jørgensen and Jobling, 1993) and, as a result, reduced growth compared with fish swimming
193 against a current at moderate velocities (Fig. 2). The spontaneous behaviour and aggressivity
194 of fishes also depends on other factors, such as rearing density (Christiansen et al., 1991;
195 Jørgensen et al., 1993; Larsen et al., 2012; McKenzie et al., 2012) and access to feed
196 (Jørgensen et al., 1996), which can also affect their growth (Jobling et al., 1993). Overall,
197 spontaneous swimming behaviour of fishes may be a significant factor in determining how a
198 current influences growth rates (Christiansen and Jobling, 1990; Larsen et al., 2012;
199 McKenzie et al., 2012; Skov et al., 2015).

200 **Mechanisms for increased growth**

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

205 fish kept in still water and those swimming at intermediate swimming velocities, 0.5 to 2 BL
206 s^{-1} (Davison and Herbert, 2013). Swimming exercise can stimulate appetite (Fig. 2) to match
207 the increased metabolic demands of locomotion, such that growth is not compromised or is
208 even increased (Christiansen and Jobling, 1990; Jørgensen and Jobling, 1993; Khan et al.,
209 2014; Leon, 1986; Li et al., 2016; Skov et al., 2015; Totland et al., 1987). In fact, fish species
210 may be able to exercise constantly at velocities between 0.5 to 2 BL s^{-1} without any decline in
211 growth rate, by compensating with increased feed intake. This, of course, implies
212 progressively reduced feed efficiency and FCR as swimming speed increases (Kießling et al.,
213 1994, 2005; Khan et al., 2014; Skov et al., 2015; Table 1).

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

227 **Future directions and considerations**

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

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

238 Research efforts on the effects of exercise should also consider diet formulation, in
239 particular to increase non-protein energy to fuel the metabolic costs of swimming, such that
240 dietary protein can be retained and allocated towards growth. Magnoni et al. (2013)
241 emphasized the need for research into how dietary lipids and carbohydrates are used to fuel
242 sustained swimming in fishes. There have been some studies investigating how swimming
243 fish use fuels (Kieffer et al., 1998; Lauff and Wood, 1997; Liew et al., 2012; Richards et al.,
244 2002). The work of Alsop and Wood (1997) demonstrated an increased reliance on non-
245 protein energy sources to fuel metabolism with increasing swimming speeds in rainbow trout
246 (*Oncorhynchus mykiss*). Skov et al. (2015) made a similar observation, noting that the
247 nitrogen quotient in rainbow trout was reduced by 20% in trout swimming against a current at
248 1 BL s^{-1} , compared to trout held in still water (0 BL s^{-1}). Although this was beneficial in
249 reducing the relative reliance on protein as fuel, overall fuel use was higher in the trout held in
250 a swimming current. Interestingly, carbohydrate may contribute 40% of the metabolic cost of
251 swimming at intermediate speeds, despite carbohydrate only making up ~10% of the energy
252 reserves of a fish (Magnoni et al., 2013). In studies by Ibarz et al. (2011) and Sánchez-
253 Gurmaches et al. (2013), an increase in dietary carbohydrate content had beneficial effects on
254 the growth of gilthead seabream (*Sparus aurata*) reared with a swimming current. This may
255 be linked to increased uptake and use of carbohydrates as fuel in skeletal muscle, which
256 promotes a protein-sparing effect, as reported for rainbow trout (Felip et al., 2012; Skov et al.,
257 2015). Nutritional optimisation is, therefore, a topic that is certainly worthy of further
258 investigation.

259 **Exercise and mitigation: links with welfare**

260 Welfare is an extremely important element of successful intensive aquaculture, being a broad
261 concept that embraces both the physical and mental well-being of an animal. A pragmatic
262 definition of 'good welfare' is that an animal is healthy and has what it 'wants' (Dawkins
263 2008). This definition encompasses the three alternative definitions of animal welfare (Fraser,
264 2008) based on function, feelings and nature, where animals should have positive natural
265 experiences similar to those in the wild. In food production aquaculture, the function-based
266 definition tends to dominate (Huntingford et al., 2006), whereby basic biological functions
267 like health, growth and reproduction are optimised under rearing conditions. There are a

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

270 **Exercise and stress**

271 There has been significant interest in whether exercise can improve welfare of intensively
272 farmed fishes by alleviating stress, encouraged by the evidence that moderate aerobic exercise
273 can provide relief against stress in mammals and humans (Eliot et al., 1976; Tsatsoulis and
274 Fountoulakis, 2006). Stress, in its strictest sense, is an endocrine condition that indicates
275 activation of the hypothalamic-pituitary axis that, in fishes, elicits a release of the steroid
276 stress hormone cortisol. Stress can also, however, have a broader definition than the endocrine
277 stress response; it can be considered to comprise any condition that causes deviations from
278 homeostasis that can engender a decline in performance and welfare of animals (Schreck and
279 Tort, 2016; Schulte, 2014). Therefore, markers of ‘stress’ can include increased metabolic
280 energy (and hence oxygen) demands or deviations in blood chemistry homeostasis, and
281 reductions in ‘fitness indicators’ such as swimming performance itself, growth rates or
282 tolerance of disease (Schreck and Tort, 2016; Schulte, 2014). For fishes in aquaculture, it is
283 widely recognised that factors such as non-optimal stocking densities or the formation of
284 dominance hierarchies can cause chronic stress (Barton and Iwama, 1991; Schreck and Tort,
285 2016). It has also been suggested that not allowing active fishes, such as salmonids, the option
286 to exercise against a current may, in itself, be intrinsically stressful (Rodnick and Planas,
287 2016).

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

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

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

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

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

326 **Exercise and immunity**

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

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

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

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

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

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

366 **Exercise, cognition and neural plasticity**

367 Given the desire to ensure optimal welfare in intensively-farmed fishes, there has been inter-
368 est in whether stimulating aerobic exercise with a current can promote neurogenesis, neuro-
369 plasticity and cognition (Huntingford and Kadri, 2013). Such effects of exercise are well-es-
370 tablished in mammals (Cotman and Berchtold, 2002; van Praag, 2008). In adult rodents, for
371 example, voluntary exercise promotes neurogenesis and expression of neurotrophins, particu-
372 larly in the hippocampus (Cotman and Berchtold, 2002; Soya et al., 2007). The hippocampus
373 plays an important role in relational memory and spatial orientation (Broglia et al., 2015) and
374 exercised mammals show increased cognitive performance in maze tests compared to seden-
375 tary conspecifics (Ma et al., 2017; van Praag, 2008; Vaynman et al., 2004). While neurogene-
376 sis in the adult mammalian brain occurs at relatively low rates and only in discrete brain ar-
377 eas, fishes exhibit neurogenesis in a multitude of brain areas throughout their lifespan
378 (Zupanc, 2006; Zupanc and Sîrbulescu, 2011). This fact was a particular stimulus for investi-
379 gating whether exercise-induced enhancement of neurogenesis and cognition also occurs in
380 fishes (Huntingford and Kadri, 2013).

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

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

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

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

407 **Exercise and sexual maturation**

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

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

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

435 This has stimulated research into whether a sustained exercise regime can prevent
436 precocious maturation in farmed fishes. Graziano et al. (2018) showed that exercise at U_{opt}
437 resulted in delayed testicular development in male European sea bass. The gonado-somatic
438 index was lower, testicular development was delayed and the expression of genes involved in
439 testicular development was down-regulated in exercised as compared to non-exercised fish.
440 Waldrop et al. (2018) found that male Atlantic salmon exercised at swimming speeds of 1.5 to
441 2.0 BL s^{-1} showed significantly less precocious maturation than those swimming at a speed
442 lower than 0.5 BL s^{-1} (6.5% and 11.5%, respectively).

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

452 **Swimming behaviours as Operational Welfare Indicators**

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

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

472 **Exercise and selection: creating more robust strains?**

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

485 Heritability measures the fraction of phenotypic variance that can be attributed to
486 genetic variation and ranges from 0 (none can be attributed) to 1 (all is attributed). In brown
487 trout (*Salmo trutta*) and Atlantic salmon, heritability of U_{crit} was moderate with large error
488 terms, namely 0.34 ± 0.22 (Blanc and Toulorge, 1981) and 0.24 ± 0.16 (Hurley and Schom,
489 1984), respectively. Similar heritability estimates of 0.24 ± 0.19 were reported for the guppy
490 *Poecilia reticulata* Peters 1859 (Nicoletto, 1995). In the threespine stickleback *Gasterosteus*
491 *aculeatus* L. 1756, heritability of burst swimming speed was relatively high at two months of

492 age (0.37-0.41) but had fallen to almost zero at 3.6 months in the same individuals, raising
493 questions about the validity of the results (Garenc et al., 1998). In the European sea bass,
494 heritability of relative maximum burst swimming speed (in BL s⁻¹) was quite high, at 0.55 ±
495 0.08 (Vandeputte et al., 2016), with a very high (0.96) genetic correlation between two
496 independent evaluations of the trait, on the same fish at 5-day intervals.

497 Genetic correlations between swimming performance and other traits have been
498 studied very little. There were weak positive correlations (0.23) between absolute maximum
499 sustained swimming speed and body mass in Atlantic salmon (Hurley and Schom, 1984) and
500 in European sea bass (0.12; Vandeputte et al., 2016). In European sea bass, maximum
501 swimming speed in BL s⁻¹ was negatively correlated with body mass, and this was true of all
502 genetic (-0.64), phenotypic (-0.56) and environmental (-0.45) correlations (Vandeputte et al.,
503 2016). This suggests that the negative relationship between body size and relative swimming
504 speed is purely phenotypic, as has already been established in fishes (Bainbridge, 1958;
505 Beamish, 1978; Bellwood & Fisher, 2001). In European sea bass, there was a weak negative
506 genetic correlation (-0.10 ± 0.19) but no phenotypic correlation (0.01) between relative
507 swimming speed and cortisol response to confinement stress, indicating that these two traits
508 are independent in this species (Vandeputte et al., 2016). The same study also found no
509 difference in relative or absolute swimming speed between the offspring of wild,
510 domesticated (1 generation) or growth selected (1 generation) parents, confirming moderate
511 links between swimming capacity and the genetic bases of growth.

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

520 **Conclusions**

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

524 whether swimming exercise can mitigate chronic stress in all species. Whether exercise can
525 promote immunity and cognition is an interesting question that is worth exploring further,
526 because there are clear potential applications in terms of welfare of farmed fishes. The
527 evidence that exercise can inhibit precocious sexual maturation is also very promising, so this
528 is another area where research should be encouraged. The use of swimming behaviour as
529 OWI is of clear potential value to the fish farmer, especially for early life stages, so further
530 studies on a broader range of species would be valuable. Finally, using exercise to select
531 robust phenotypes, or to counteract debilitating effects of a historical selection for rapid
532 growth, also requires further investigation. Overall, therefore, further research is required, in
533 concert with fish farmers, to develop methods to exercise fishes in culture, or to use exercise
534 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	3812±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	
<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		19	
		27		1.5-2.4		3*	
		26		2.4-3.6		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				

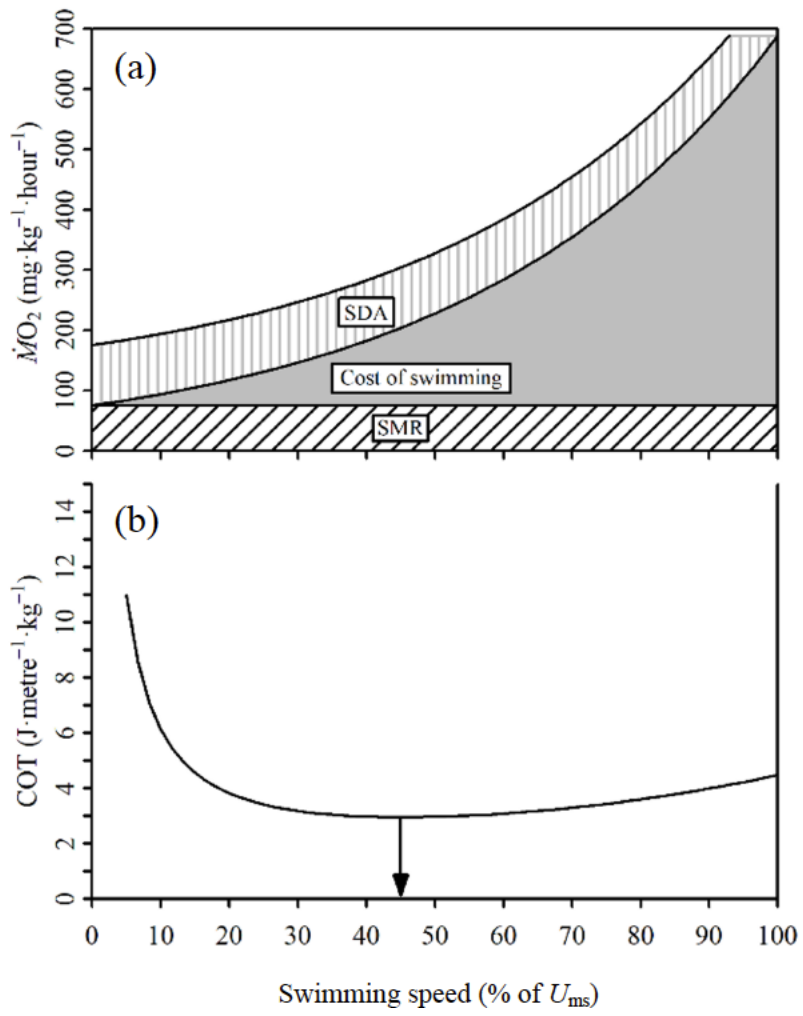
No effect on plasma cortisol							
<i>O. mykiss</i>	242		0.0	25	60	1	(McKenzie et al., 2012)
	236		0.9			1	
	223		0.0	100		<1	
	224		0.9			<1	
<i>Atractoscion nobilis</i>	42	108	0.0	6.9	42		(Peters, 2009)
			1.3				
			2.0				
<i>Seriola lalandi</i>	34	84	0.0	7.6	34		(Peters, 2009)
			1.4				
			2.1				
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.

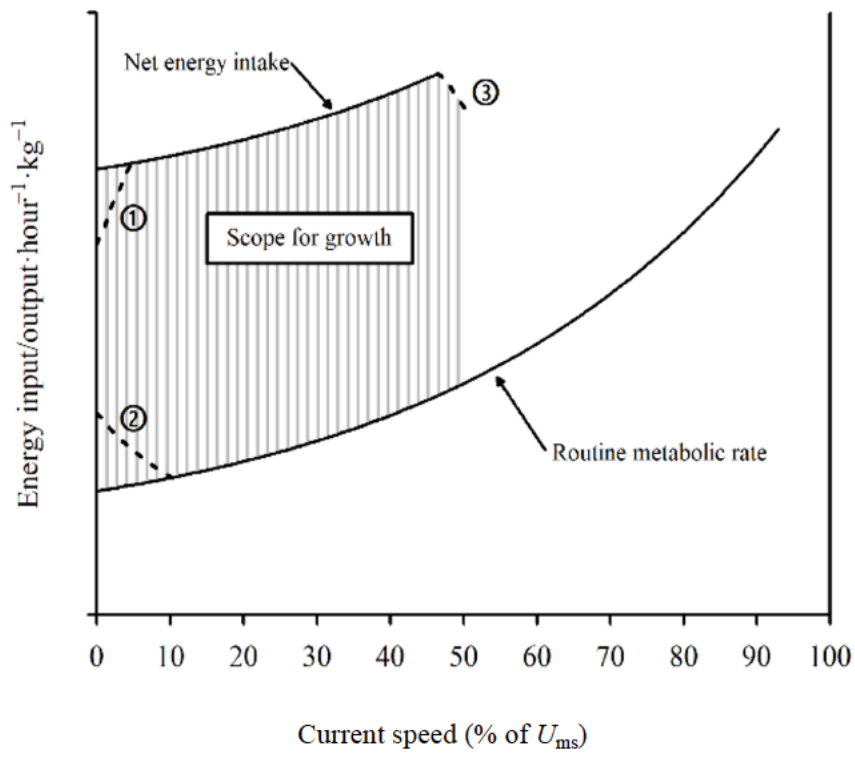
1004 **Figure 2.** A conceptual model of the interplay among metabolic rate, feed intake and scope
1005 for growth in fish. At low velocities feed intake ① may or may not be reduced, and/or
1006 metabolic rate increased ②, due to increased levels of spontaneous activity or aggression. As
1007 a result, 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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