Accommodating the cost of growth and swimming in fish—the applicability of exercise-induced growth to juvenile hapuku (Polyprion oxygeneios)

Javed R. Khan1*, Caroline Trembath2, Steve Pether3, Michael Bruce3, Seumas P. Walker3 and Neill A. Herbert1

1 Leigh Marine Laboratory, Institute of Marine Science, The University of Auckland, Auckland, New Zealand
2 Bay of Plenty Polytechnic, Tauranga, New Zealand
3 National Institute of Water and Atmospheric Research, Bream Bay Aquaculture Park, Ruakaka, New Zealand

Edited by:
Arjan P. Palstra, Wageningen University and Research Centre, Netherlands
Reviewed by:
Peter Vilhelm Skov, Technical University of Denmark, Denmark
Christian Tudorache, Leiden University, Netherlands
*Correspondence:
Javed R. Khan, Leigh Marine Laboratory, Institute of Marine Science, The University of Auckland, PO Box 349, Warkworth 0941, New Zealand
e-mail: jkha022@aucklanduni.ac.nz

Induced-swimming can improve the growth and feed conversion efficiency of finfish aquaculture species, such as salmonids and Seriola sp., but some species, such as Atlantic cod, show no or a negative productivity response to exercise. As a possible explanation for these species-specific differences, a recent hypothesis proposed that the applicability of exercise training, as well as the exercise regime for optimal growth gain (ERopt growth), was dependent upon the size of available aerobic metabolic scope (AMS). This study aimed to test this hypothesis by measuring the growth and swimming metabolism of hapuku, Polyprion oxygeneios, to different exercise regimes and then reconciling the metabolic costs of swimming and specific dynamic action (SDA) against AMS. Two 8-week growth trials were conducted with ERs of 0.0, 0.25, 0.5, 0.75, 1, and 1.5 body lengths per second (BL s⁻¹). Fish in the first trial showed a modest 4.8% increase in SGR over static controls (BL s⁻¹). Fish in the first trial showed a modest 4.8% increase in SGR over static controls whereas the fish in trial 2 showed no significant effect of ER on growth performance. Reconciling the SDA of hapuku with the metabolic costs of swimming showed that hapuku AMS is sufficient to support growth and swimming at all ERs. The current study therefore suggests that exercise-induced growth is independent of AMS and is driven by other factors.

Keywords: exercise training, swim-flume respirometry, aerobic metabolic scope, optimal swim speed, cost of transport

INTRODUCTION

There is ample evidence in the literature showing that induced swimming, or exercise training, can improve the growth and feed conversion efficiency of many species of farmed fish (Davison, 1989; Palstra and Planas, 2011; Davison and Herbert, 2013). Most of this evidence has been accumulated in the salmonid groups Oncorhynchus (Houlihan and Laurent, 1987; Aslop and Wood, 1997; Hernández et al., 2002), Salmo (Davison and Goldspink, 1977; Totland et al., 1987; Boesgaard et al., 1993) and Salvelinus (Leon, 1986; Christiansen et al., 1989; Christiansen and Jobling, 1990) but there are examples of exercise-induced growth from other groups, with species such as the striped bass Morone saxatilis (Young and Cech, 1993) and the yellowtail kingfish Seriola lalandi (Brown et al., 2011). The global aquaculture industry is expanding rapidly and the potential for continuous exercise to accelerate the growth of fish has direct application due to the potential for fast biomass gain, improved flesh quality and the flexibility of production it can provide. However, exercise-induced growth is often perceived as a paradoxical concept as it seems illogical that fish can expend considerable energy on exercise whilst also committing to the extra expense of accelerated growth. This view is reinforced by a number of studies showing that exercise has either nil, or only negative effects on the growth of fish such as the Atlantic cod Gadus morhua (Bjørnevik et al., 2003) and Chinook salmon Oncorhynchus tshawytscha (Kiesling et al., 1994). Therefore, to stand any chance of exploiting the economic gains of exercise-induced growth in aquaculture, an in-depth understanding of how fish balance the metabolic costs of growth and exercise needs to be ascertained, particularly in the case of information-poor species that are new to farming.

There has been a rekindled interest in the mechanisms and applicability of exercise-induced growth in recent years (Palstra and Planas, 2011) and new efforts have been made to predict the levels of exercise required for the best rate of growth in novel species using readily accessible measures of behavior and physiology (Davison and Herbert, 2013; Herbert, 2013). In particular, the aerobic metabolic scope (AMS) of fish and the speed where the energetic cost of transport (COT) is at its lowest, termed the optimal swimming speed (Uopt), appears to explain a significant proportion of the variation between different fish that show exercise-induced growth (Davison and Herbert, 2013). AMS is the difference between maintenance and maximal metabolic rates, and thus represents a physiological framework, within which non-maintenance physiological work operates (Jobling, 1994; Clark et al., 2013). In light of this belief, it has been suggested that a larger AMS better accommodates the energetic costs
of swimming in addition to other processes, such as protein synthesis associated with growth and feeding (von Herbing and White, 2002; Davison and Herbert, 2013). There are few experimental studies on this topic but the work of Owen (2001) on the European eel Anguilla anguilla appears to support this assertion. Indeed, where AMS was insufficient, or the costs of feeding (specific dynamic action, SDA) were deemed excessive, the swimming speed of eels were reduced to accommodate SDA as a form of energetic prioritization (Owen, 2001). On the basis of these observations, Davison and Herbert (2013) examined how the required exercise regime for optimal growth acceleration (termed ERopt growth, in units of body lengths s−1, BL s−1) co-varied with AMS in a variety of well-studied species. As a positive but non-linear correlation was found between ERopt growth and AMS, it is hypothesized to provide the metabolic capacity for optimal exercise-induced growth in the vicinity of ERopt growth, in units of body lengths s−1 at 17 °C, based on the data of Khan et al., 2014) is hypothesized to provide the metabolic capacity for optimal exercise-induced growth in the vicinity of 0.4–0.5 BL s−1 (Herbert, 2013). If exercise-induced growth is indeed observed in hapuku, Uopt and ERopt growth should also be relatively well matched (Davison and Herbert, 2013). As a further step in this validation and testing process, the metabolic costs of swimming at different speeds and the recently measured cost of SDA (Khan et al., in press), which is largely comprised of post-absorptive protein synthesis and growth (Secor, 2009; Seth et al., 2010) was also reconciled against the available AMS. This allowed for the experimental resolution of whether hapuku have metabolic capacity to accommodate swimming and the physiological costs associated with growth.

**MATERIALS AND METHODS**

**SPECIMENS, TAGGING, AND GROWTH TRIALS**

Two full- and half-sibling groups of ~120 juvenile hapuku (P. oxygeneios, ~8 months post-hatch, 240 in total) were used for growth trials at the NIWA Bream Bay Aquaculture Facility in Ruakaka, Northland, New Zealand. “Trial 1” fish (128.8 g ± 3.1 g) were hatched 12 weeks prior to “trial 2” fish (172.4 ± 4.5 g) and were also smaller at the start of the growth trials as they were 4 weeks younger at the point when they entered the experimental tanks. Both groups of fish were held at 17°C in larger than 4 m³ tanks prior to the start of both trials. To track the growth and performance attributes of individuals, all fish were tagged intraperitoneally with a 5 mm passive integrated transponder (PIT) under anesthesia (0.01 mL L−1 Aqui-S® followed by 0.3 mL L−1 2-phenoxyethanol, standard facility practice). Specimens were treated with chloramine-T (0.005 mL L−1) to prevent infection post-tagging (added to flowing tank water, standard facility practice). Any individuals that showed signs of infection were treated further with formalin (0.15 mL L−1) or euthanized with an excessive dose of Aqui-S® (0.1 mL L−1). Thereafter, two sequential and identical growth trials were conducted incorporating six different exercise regimes (ER, corresponding to six in-tank flow speeds of 0.0, 0.25, 0.5, 0.75, 1, and 1.5 body lengths per second, BL s−1). Each of the two trials were conducted in six identical 1.6 m³ circular tanks (560 mm water depth, 1900 mm diameter). All tanks were housed in a purpose-built building under ambient light conditions (11L: 13D) and supplied with fresh 1 µm filtered and UV-sterilized (ALX2/8, 150 mW cm−2, Davey Water Products, Australia) seawater at 17 ± 0.3°C. A continuous non-directional inflow of water (30 L min−1) was present at the side of each tank and all tanks were central draining. Water flow around the tank was negligible in the 0.0 BL s−1 (control) tank but the remaining water flow ER treatments (i.e., 0.25, 0.5, 0.75, 1, and 1.5 BL s−1) were maintained through the use of external water pumps (Leader® Ecopool 15, Leader Pumps, Italy) plumbed over the side of each tank via a 25 mm PVC intake and outlet. Pump outlets were connected to a spray bar at a water depth level of 100 mm from the surface and the spray bar extended 500 mm into the tank at a perpendicular angle. Water flow through the spray bars (and thus flow speed in the tanks) was controlled through a ball valve plumbed between the pumps and the spray bars. Flow speeds were set in the tanks by measuring water velocity (in m s−1) 200 mm from the tank wall at 100 mm depth on the side directly opposite the spray bar with a Höntzsch® HFA anemometer (V 1.5, Höntzsch technologies, Waiblingen, Germany) and making the necessary correction to the flow of water according to the average body length of the fish at regular fortnightly intervals. Each tank had a single projection of PVC pipe (200 mm high, 100 mm diameter) off the floor, approximately half way between the wall and the center. They were entirely submerged, impossible to remove and created a small low-flow area in their wake. Water chemistry was checked regularly and remained at normal levels at all times throughout both trials.

The fish intended for trial 1 were anesthetized (as described above) in their pre-trial holding tank at 17 ± 0.3°C and their initial weight and length were measured. They were then divided randomly and evenly (~20 per tank) into one of the six experimental tanks and allowed to recover for 4 h with no directional flow. Once swimming behavior appeared normal, flow speeds in the tanks were increased slowly toward one of the six exercise training speeds in BL s−1 according to the average BL of all
RESPIROMETRY

Swim flume respirometry was performed on fish from three ER treatments (0.0, 0.75, and 1.5 BL s\(^{-1}\)) to resolve the effect of exercise training on metabolic cost functions. Aside from understanding the potential metabolic effects of long-term exercise, this information was important for reconciling the cost of growth and swimming. All specimens were starved for 48 h prior to respirometry to remove any confounding effects of feeding on metabolic rate (Ross et al., 1992; Thuy et al., 2010). The mass specific rate of oxygen consumption (MO\(_2\), mg O\(_2\) kg\(^{-1}\) h\(^{-1}\)) was then determined from 24 fish from trial 2 (i.e., 8 fish from the 0.0, 0.75 and 1.5 BL s\(^{-1}\) ER groups) over a period of 30 days in the 38.4 L Brett-type swim flume respirometer described by Brown et al. (2011). The change in oxygen saturation in the respirometer was measured continuously using a Firesting\textsuperscript{®} 2-channel oxygen meter (Pyroscience, Germany) connected to an oxy-dipping probe (Pyroscience, Germany) which was sealed into the respirometer in a position anterior to the swimming section. The respirometer was operated through a custom software interface which controlled water flow speed in the swimming section and the cycling of the flush, wait and measure periods (5, 1 and 4 min, respectively, 10 min total). MO\(_2\) and its components were calculated using the same formulae as Brown et al. (2011).

After measuring the weight, length, depth, and width of fish [to compensate for the solid-blocking effect (Steffensen, 1989)], specimens were placed in the sealed swimming section of the respirometer (530 × 130 × 155 mm). This occurred at ~1600 h and provided fish an overnight period of acclimation to the conditions of the respirometer with a low flow of water (0.25 BL s\(^{-1}\)) and with the system cycling automatically through a repeated series of flush, wait and measure. From 0800 the following day, a critical swimming speed (\(U_{\text{crit}}\)) test commenced where the flow speed inside the swimming section was increased by 0.25 BL s\(^{-1}\) every 30 min (i.e., after three 10 min flush-wait-measure cycles). This continued until 1/3 of the body length specific oxygen consumption levels were measured without a fish and confirmed that bacterial respiration was essentially nil and negligible in all runs. All equipment was cleaned thoroughly between experiments with freshwater and a mild hypochlorite solution (0.005 g L\(^{-1}\)).

For each individual fish, critical swimming speed (\(U_{\text{crit}}\)) was calculated using the same formula as Brett (1964), Brown et al. (2011), and Yanase et al. (2012). The 15% quantile method of Chabot and Claireaux (2008) and Franklin et al. (2013) was used to obtain a near-resting value of MO\(_2\) from overnight measures at 0.25 BL s\(^{-1}\) in order to remove erroneously-low values associated with unusually weak oxygen probe signals. Thereafter, three MO\(_2\) values obtained from each of the three flush-wait-measure cycles at each speed were averaged to resolve the relationship between swimming speed and MO\(_2\) (Korsmeyer et al., 2002; Brown et al., 2011) at speeds that were considered to be exclusively aerobic, i.e., up to 2.5 BL s\(^{-1}\) (Roche et al., 2013). In order
to yield an estimate of standard metabolic rate (MO2_standard) for every individual fish, average MO2 at all speeds was extrapolated back to 0.0 BL s^{-1} using an exponential regression function as used previously by other authors (Pettersson and Hedenström, 2000; Yanase et al., 2012) as power functions underestimated MO2_standard values compared to other investigations on the same species (Khan et al., 2014, in press). Using all MO2 values from the point that fish first entered the respirometer, MO2_{max} was calculated using the 99% quantile method of Khan et al. (2014) as this yielded higher, and produced less inter-individual variation, than MO2 values at U_{crit}. AMS was calculated by subtracting MO2_standard from MO2_{max} and the gross cost of transport (GCOT, mg O2 kg^{-1} BL^{-1}) was calculated by dividing MO2 by their corresponding swimming velocity (BL s^{-1}).

**STATISTICAL ANALYSES**

The data relating the effect of ER treatments on SGR, ΔCF, FCR and feed per individual (g) from trial 1 and 2 were each initially described with a second-order (non-linear) polynomial regression of the form: \( y = ax^2 + bx + c \). Non-linear polynomial regressions were also used to test the effect of ER on GCOT, as well as being used to calculate \( U_{opt} \) (Pettersson and Hedenström, 2000). Exponential regressions were used to analyse the effect of ER on the relationship between MO2 and swimming speed. Due to the presence of non-normal data, the effect of ER on SGR and ΔCF in both trials was tested with a non-parametric Kruskal–Wallis One-Way analysis of variance (ANOVA) test. When this test identified a significant effect of ER, a Dunn’s comparison test was then used to locate a specific post-hoc difference in SGR or ΔCF from the control 0 BL s^{-1} ER treatment. After ensuring that data was compliant for normality and homoscedasticity, a repeated measures (RM) Two-Way ANOVA was used to test the effect of swim speed on MO2 (factor 1) as well as the effect of long-term ER on MO2 (factor 2). The same Two-Way RM ANOVA was also used to test the effect of the same two factors on GCOT. The optimal (i.e., least cost) swimming speed (\( U_{opt} \)) of individual fish was calculated from the non-linear speed-GCOT regression and taken as the speed that yielded a minimum level of GCOT. The effect of long-term ER on \( U_{opt}, MO2_{standard}, MO2_{max}, AMS, \) and \( U_{crit} \) was then tested with individual One-Way ANOVA tests, followed by a Tukey post-hoc test for specific pairwise comparisons where appropriate. Significance was accepted at \( P \leq 0.05 \) and all data are displayed ± standard error. All statistical analyses were performed using SigmaPlot® version 11.0.

**RESULTS**

**EFFECTS OF EXERCISE TRAINING ON JUVENILE HAPUKU GROWTH**

Non-linear regressions did not provide convincing evidence that ER was positively linked with weight-specific growth (SGR) for either trial 1 (\( F = 1.91, R^2 = 0.56, P > 0.05 \)) or trial 2 (\( F = 0.56, R^2 = 0.27, P > 0.05 \)) (Figure 1A). Kruskal–Wallis tests confirmed that ER did not have any effect on the SGR of fish in Trial 2 (\( H = 5.23, P > 0.05 \)) where starting weights were higher (Table 1) but a strong positive effect of ER on the SGR of fish in trial 1, where starting weights were lower, was identified (\( H = 18.93, P < 0.01 \)) (Figure 1A and Table 1). Specific post-hoc comparisons against the control 0.0 BL s^{-1} treatment revealed that
fish were subject to a significant 3.5% increase in SGR at 0.5 BL s\(^{-1}\) (P < 0.05) and a 4.8% increase in SGR at 0.75 BL s\(^{-1}\) (P < 0.05) (Figure 1A). No other ER treatment was subject to a change in SGR.

The regressions detailing the link between ER and ΔCF were non-significant within the scale of responses observed in trial 1 (F = 1.33, \(R^2 = 0.47, P > 0.05\)) and trial 2 (F = 0.65, \(R^2 = 0.3, P > 0.05\)) (Figure 1B). ANOVA tests revealed that ΔCF was positively affected by increasing ER in both trial 1 (H = 12.29, P < 0.05) and trial 2 (H = 13.76, P < 0.05). However, specific post-hoc comparisons against the 0.0 BL s\(^{-1}\) control only revealed a significantly higher ΔCF following long-term swimming at 0.5 BL s\(^{-1}\) in trial 1 (Figure 1B). Therefore, in addition to the positive effect on SGR, fish at 0.5 BL s\(^{-1}\) had a relatively deeper body shape.

FCR varied little as a function of ER across trial 1 (F = 4.98, \(R^2 = 0.77, P > 0.05\)) and trial 2 (F = 1.67, \(R^2 = 0.53, P > 0.05\)) (Figure 1C). Feed intake per individual (g) was positively related to ER in trial 1 fish (F = 115.48, \(R^2 = 0.98, P < 0.05\)) but showed no relationship with ER in trial 2 (F = 0.78, \(R^2 = 0.34, P > 0.05\), Figure 1D).

**EFFECTS OF EXERCISE TRAINING ON THE SWIMMING PERFORMANCE OF JUVENILE HAPUKU**

\(MO_2\) increased linearly with swimming speed for each of the 0.0, 0.75, and 1.5 BL s\(^{-1}\) ER groups (linear regressions with \(R^2 = 0.78, R^2 = 0.78, R^2 = 0.76\), and \(P < 0.05\) for the 0.0, 0.75, and 1.5 BL s\(^{-1}\) ER groups, respectively, Figure 2A) and a highly significant effect of swimming speed on \(MO_2\) was confirmed from the Two-Way RM ANOVA tests (F = 136.11, \(P < 0.01\)). There was, however, no significant difference in \(MO_2\) between the three ER treatments (F = 1.41, \(P > 0.05\)) and there was no significant interaction between swimming speed and ER on \(MO_2\) (F = 0.61, \(P > 0.05\)).

\(GCOT\) showed a significant parabolic relationship with swimming speed for each of the 0.0, 0.75, and 1.5 BL s\(^{-1}\) ER groups (\(R^2 = 0.74, R^2 = 0.73, R^2 = 0.73\), and \(P < 0.05\) for the 0.0, 0.75, and 1.5 BL s\(^{-1}\) ER groups, respectively, Figure 2B) and a highly significant effect of swimming speed on \(GCOT\) was once again confirmed with the Two-Way RM tests (F = 138.47, \(P < 0.01\)). However, there was no significant difference in \(GCOT\) between the three ER groups (F = 0.51, \(P > 0.05\)) and there was no interactive effect of swimming speed and ER on \(GCOT\) (F = 0.46, \(P > 0.05\)). \(U_{opt}\) estimations were also not significantly different between the three ER treatments (F = 1.26, \(P > 0.05\)) and were essentially identical to the pooled \(U_{opt}\) estimation of 1.86 BL s\(^{-1}\) with a \(GCOT_{min}\) of 0.03 mg O\(_2\) kg\(^{-1}\) BL\(^{-1}\).

Long-term exposure to the three ER treatments had no significant effect on \(MO_2\) standard (F = 1.17, \(P > 0.05\), \(MO_2\) max (F = 1.15, \(P > 0.05\)), AMS (F = 0.75, \(P > 0.05\)), or \(U_{crit}\) (F = 2.63, \(P > 0.05\)) (Table 2).

**Table 1** The starting weight (g), final weight (g), total feed consumed (g), and number of fish in each of Trial 1 and Trial 2.

| Tank speed (BL s\(^{-1}\)) | Start weight (g) | End weight (g) | N     | Total feed intake (g) | Start weight (g) | End weight (g) | N     | Total feed intake (g) |
|---------------------------|-----------------|----------------|-------|-----------------------|-----------------|----------------|-------|-----------------------|
| 0.0                       | 119.9 ± 3.1     | 341.4 ± 10.1   | 20    | 4331.4                | 170.2 ± 6.1     | 382.6 ± 12.1   | 17    | 3635.2                |
| 0.25                      | 131.4 ± 4.7     | 366.7 ± 9.9    | 19    | 4360.1                | 170.2 ± 8.0     | 372.8 ± 5.6    | 17    | 3359.3                |
| 0.5                       | 128.6 ± 4.6     | 380.6 ± 12.6   | 20    | 4702.2                | 170.9 ± 5.7     | 3972 ± 14.1    | 17    | 3841.9                |
| 0.75                      | 122.7 ± 4.6     | 366.2 ± 11.8   | 19    | 4576.2                | 1875.5 ± 10.6   | 423.8 ± 19.7   | 17    | 4205.7                |
| 1.0                       | 133.0 ± 4.3     | 375.8 ± 7.1    | 16    | 4015.2                | 1718 ± 10.1     | 388.4 ± 19.0   | 17    | 3678.9                |
| 1.5                       | 138.8 ± 3.1     | 381.9 ± 7.6    | 17    | 4384.3                | 1674 ± 6.2      | 372.3 ± 6.2    | 17    | 3732.4                |

All values shown ± standard error.
OOS study for fish fed a 1.5% BW diet (Khan et al., in press). An estimate of SDA at 17°C (Table 2) was attributed to their active ecotype, as indeed, hapuku with an average starting weight of 130 g in exercise in the region of 0.75–1.5 BL s⁻¹ are reportedly show a critical swimming speed at 17°C (Davison and Goldspink, 1982). A summary of hapuku metabolic costs across a temperature range of 15–24°C was amalgamated and graphically represented (Figure 3) for the purpose of reconciling metabolic components against available AMS at 17°C. MO₂standard values for 15°C and 21°C were measured in a different study in similarly sized fish using a static respirometry system (Khan et al., in press) and the line between these two values intersected 17°C at 91.31 mg O₂ kg⁻¹ h⁻¹ which is very similar to the MO₂standard estimate from the current study (87.53 ± 5.21 mg O₂ kg⁻¹ h⁻¹) at 17°C (Table 2). SDA estimates were also measured in the same previous study for fish fed a 1.5% BW diet at both 15 and 21°C (Khan et al., in press). An estimate of SDA at 17°C was then interpolated from the straight line function between these two SDA values (Q10 = 3.44, MO₂ = 25.45temp – 242.95). It was therefore assumed that peak SDA follows a linear relationship between these two temperatures when fed the same-sized ration. (NB. ration size varied 1.3–1.8% BW diet in the current study so was close to the standard 1.5% BW ration in Khan et al., in press). ER had no significant effect on swimming costs at 17°C (see above) so the MO₂ values from each ER were pooled to calculate an average cost of swimming at 0.25, 0.5, 0.75, 1.0, and 1.5 BL s⁻¹. MO₂ values are shown as the highest and lowest estimates from the current study (i.e., 1.5 BL s⁻¹ = 337.90 ± 8.59 mg O₂ kg⁻¹ h⁻¹ and 0.75 BL s⁻¹ = 294.05 ± 5.99 mg O₂ kg⁻¹ h⁻¹, respectively, Table 2).

## DISCUSSION

In order to validate the model of Davison and Herbert (2013), exercise-induced growth in juvenile hapuku would be expected in the range of ∼0.4–0.5 BL s⁻¹. However, the current does not provide compelling evidence of exercise-induced growth at 17°C (Figure 1) which is a stark contrast to salmonids that reportedly show a ≤40% increase in growth from sustained exercise in the region of 0.75–1.5 BL s⁻¹ (Davison and Goldspink, 1977; Houlihan and Laurent, 1987; Jorgensen and Jobling, 1993). Indeed, hapuku with an average starting weight of 130 g in Trial 1 only showed a maximum of a 4.8% increase in growth at 0.5 and 0.75 BL s⁻¹, respectively, (Figure 1A) whereas the larger 170 g (starting weight) hapuku showed no sign of exercise-induced growth in Trial 2 (Table 1). Earlier studies on salmonids considered that the ER at which optimal growth is ascertainment (i.e., ERopt growth) was attributed to their active ecotype, as well as the physiological and behavioral requirements of schooling, migration and river spawning [e.g., position holding in strong water flows (Jobling et al., 1993)]. Hapuku would not be described as highly active so the data is consistent with

### Table 2 | The average weight (g), standard metabolic rate (MO₂standard), maximum metabolic rate (MO₂max), and aerobic metabolic scope (AMS) of juvenile hapuku (measured as mg O₂ kg⁻¹ h⁻¹) as well the critical swimming speed (Ucrit, BL s⁻¹) of juvenile hapuku raised for 6 weeks at either 0.0, 0.75, or 1.5 BL s⁻¹ and measured in a swim-flume respirometer.

| Swim speed treatment | Average weight (g) | MO₂standard (mg O₂ kg⁻¹ h⁻¹) | MO₂max (mg O₂ kg⁻¹ h⁻¹) | Critical swimming speed (Ucrit, BL s⁻¹) |
|----------------------|--------------------|------------------------------|--------------------------|---------------------------------------|
| 0.0 BL s⁻¹          | 469.12 ± 5.96      | 91.33 ± 5.37                 | 324.72 ± 7.44            | 2.72 ± 0.13                           |
| 0.75 BL s⁻¹         | 496.38 ± 8.14      | 80.58 ± 5.46                 | 294.05 ± 5.99            | 2.55 ± 0.08                           |
| 1.5 BL s⁻¹          | 481.44 ± 6.77      | 90.67 ± 5.80                 | 33790 ± 8.59             | 2.94 ± 0.14                           |

No significant effect of swimming speed treatment was detected in any of the listed variables (P > 0.05). All values shown ± standard error.
the view of Jobling et al. (1993). However, the recent review on exercise-induced growth in fish by Davison and Herbert (2013) went further to propose that $ER_{\text{opt growth}}$ is a function of AMS. Most salmonoids, with their active ecotype and high AMS ($\sim 350–500 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$), show exercise-induced growth at relatively fast swimming speeds (Walker and Emerson, 1978; Houlihan and Laurent, 1987; Jørgensen and Jobling, 1993; Bugnon et al., 2003) and therefore provide data to support the upper end of the Davison and Herbert (2013) model. In contrast, the lower end of the model is based on species such as gadoids that have a small AMS in the region of $\sim 150–200 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (Hammer, 1994; Karlsen et al., 2006) and show little to no growth response to exercise-training (Bjørnevik et al., 2003; Karlsen et al., 2006). On the basis of these observations, the current study aimed to assess the AMS – $ER_{\text{opt growth}}$ model of Davison and Herbert (2013) by testing whether the $\sim 300 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ AMS level of Khan et al. (2014) does indeed lead to an $ER_{\text{opt growth}}$ of 0.4–0.5 BL s$^{-1}$. At least for trial 1, the Davison and Herbert (2013) model prediction does appear to provide a reasonable fit. However, the lack of exercise-induced growth in trial 2 is not consistent with the Davison and Herbert (2013) model and the very modest levels of growth acceleration do not validate the model for this novel species.

The AMS values measured from 480 g hapuku at the end of the current study ranged from 213 to 247 mg O$_2$ kg$^{-1}$ h$^{-1}$ (Table 2) and are therefore lower than the 300 mg O$_2$ kg$^{-1}$ h$^{-1}$ AMS value ascertained for 180 g hapuku at 17°C in the study of Khan et al. (2014). Whilst these larger AMS values were used initially to formulate our hypothesis, the recently established values of AMS are considered more valid because they originate from a size class of fish that corresponds to the current $ER_{\text{opt growth}}$ data. However, applying these lowered AMS values to the model of Davison and Herbert (2013) predicts an $ER_{\text{opt growth}}$ of between 0.15 and 0.3 BL s$^{-1}$ which does not correspond to the observed $ER_{\text{opt growth}}$ range of fish in trial 1, or even the total lack of exercise-induced growth in trial 2 (Figure 1A). These data further suggest that the relationship between AMS and $ER_{\text{opt growth}}$ is not validated in this species.

In relation to the second model of Davison and Herbert (2013), the $ER_{\text{opt growth}}$ range observed in trial 1 (0.5–0.75 BL s$^{-1}$, Figure 1) does not even vaguely correspond to the measures of $U_{\text{opt}}$ in the current study (1.86 BL s$^{-1}$, Figure 2B). The $U_{\text{opt}}$ estimation for juvenile hapuku was unaffected by ER and is considerably higher than one might expect for a species that is less active than Atlantic salmon *Salmo salar*, brown trout *Salmo trutta*, and brook charl *Salvelinus fontinalis* which all have $U_{\text{opt}}$ values in the range of 0.9–1.1 BL s$^{-1}$ (Beaumont et al., 2000; Deitch et al., 2006; Tudorache et al., 2011). Atlantic cod and gilthead seabream *Sparus aurata* also have unusually high $U_{\text{opt}}$ estimations ranging from 1.2 to 1.6 BL s$^{-1}$ in the cod and up to 2.3 BL s$^{-1}$ in the gilthead seabream (Schurmann and Steffensen, 1997; Steinhausen et al., 2010). Alternative methods of calculating the minimum COT (i.e., those suggested by Pettersson and Hedenström, 2000) produce a similarly high $U_{\text{opt}}$ estimate of 1.84 BL s$^{-1}$ for the pooled GCOT data (Figure 2B). It may be that these less active ecotypes do not have an ecologically functional or relevant $U_{\text{opt}}$ as would be the case for migratory or highly active species (Hinch and Rand, 2000; Tudorache et al., 2011) though this is speculation and requires further investigation.

The hypothesis that AMS places a capacity limitation on exercise-induced growth (Davison and Herbert, 2013) is supported by the current data for juvenile hapuku. For 480 g hapuku at 17°C, the costs of exercise and SDA (which can be comprised of up to 80% protein synthesis (Coulson and Hernandez, 1979; Brown and Cameron, 1991; Seth et al., 2010; Li et al., 2013)) are easily accommodated within available AMS, even at the highest swimming speed used in the growth trials (1.5 BL s$^{-1}$, Figure 3). It is generally accepted that the energetic costs associated with SDA are largely comprised of post-absorptive protein synthesis and is thought to represent the costs of growth (Whitley et al., 2001; Grigoriou and Richardson, 2008; Secor, 2009) and, in less active species with low AMS, SDA often consumnes a large proportion of AMS potential (Jobling, 1983; Soofiani and Priede, 1985; Jordan and Steffensen, 2007). This has led researchers to propose that an inability to reconcile the metabolic costs of growth and exercise simultaneously would either lead to a reduction in the rate of protein synthesis (as a prioritization of exercise over growth, Davison and Herbert, 2013) or, as predicted for the European eel *Anguilla anguilla* in the study of Owen (2001), a reduction in swimming activity as a prioritization of growth over exercise. Therefore, with the ability to accommodate the costs of exercise and growth simultaneously and with metabolic costs of swimming (Figure 2) and SDA not vastly different to other ecotypes (Fu et al., 2005; Jordan and Steffensen, 2007; Ohlberger et al., 2007; Yanase et al., 2012; Frisk et al., 2013), it is proposed that the weak exercise growth response of hapuku is a species-specific effect and not due to capacity limitation of aerobic metabolism.

The data in Figure 3 provides evidence that AMS does not limit the ability of juvenile hapuku to swim and grow simultaneously but, on a cautionary note, it does not take into the account the extra metabolic costs of spontaneous activity (Boisclair and Tang, 1993; Tang et al., 2000) nor does it necessarily prove that hapuku have the metabolic capacity to grow faster whilst swimming. With respect to the latter point, the SDA costs of supplementary fast growth from exercise were not measured within static respirometry chambers (Khan et al., in press) and is therefore still not yet resolved. Interestingly, there is other recent data suggesting that the costs of SDA and exercise can act additively in the darkbarbel catfish *Peltebargus vachelli* (Li et al., 2010) and the sea bass *Dicentrarchus labrax* (Altimiras et al., 2008) to the point where total costs exceed measured $MO_2_{\text{max}}$. This is relevant to the current discussion as it suggests a potential disconnect between AMS and the combined costs of exercise and growth. More importantly, this data opposes the AMS - $ER_{\text{opt growth}}$ hypothesis of Davison and Herbert (2013) as exercise and growth could potentially occur simultaneously in catfish and sea bass without their costs being limited by AMS. The presence of additive SDA has not yet been addressed in hapuku and, whilst this species appears suited to $U_{\text{crit}}$ swimming tests in a swim-flume respirometer, feeding attempts have not yet been successful. To investigate this issue further, it may be necessary to implement a gavage protocol or directly infuse food or amino acids into the gut or bloodstream (Brown and Cameron, 1991; Li et al., 2010).
CONCLUSION

The data from the current study is not consistent with the hypothesis of Davison and Herbert (2013) that AMS sets a limit to, and therefore determines, the likelihood of seeing exercise-induced growth in finfish aquaculture species such as hapuku. This was essentially based on the fact that (i) juvenile hapuku showed a modest and consistent exercise-induced growth response in a narrow band of swimming speeds (0.5–0.75 BL s\(^{-1}\)), and (ii) the AMS of these fish appears sufficient to accommodate the physiological costs SDA and swimming simultaneously. It may be that this species is generally not responsive to exercise training but, before that conclusion is reached, future research should possibly strive to examine the response of different-sized hapuku across a greater range of (optimal) temperatures as a means of disentangling the potential role of these factors in exercise-induced growth (e.g., Brown et al., 2011).

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