

A moving light stimulus elicits a sustained swimming response in farmed Atlantic salmon, *Salmo salar* L.

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Abstract The productivity and welfare benefits of sustained swimming in fish are well documented, but are not yet exploited in commercial aquaculture. We report here on a study designed to test the feasibility of inducing sustained exercise in Atlantic salmon (*Salmo salar* L.) using a novel lighting device which provides an apparently moving light pattern. It was found that such a device could induce sustained swimming in Atlantic salmon held in tanks and that a centrally-placed (inner ring) light system was far more effective in this context than one in which lights were placed on the outer wall of tanks. The central configuration was associated with enhanced rates of growth, feed conversion and reduced levels of plasma cortisol. Such developments in fish swimming technologies may assist the sustainability of finfish aquaculture through promotion of sustained exercise leading to improved productivity and welfare.

Keywords Swimming · exercise · salmon · *Salmo salar* · growth · FCR

Introduction

A considerable body of research has been directed at examining the beneficial effects of sustained exercise on fish, as reviewed by Davison (1997). Such benefits include improved growth and FCR and reduced stress and are generally restricted to more active fish species, including the most widely farmed salmonid, the Atlantic salmon, *Salmo salar* L. (Totland et al. 1987; Boesgaard et al. 1993; Jørgensen and Jobling 1993). Whilst such effects may have considerable implications for aquaculture, the only way of inducing sustained swimming to date has been through the generation of water currents, which is impractical in seacages where the main growth phase of the salmon production cycle occurs (Waller 2001). Explorations into simple alternative methods that elicit sustained exercise without the need for water currents might therefore allow the benefits of exercise to be realized with Atlantic salmon in commercial aquaculture (Juell 1995).

Like other animals, fish show a strong response to moving visual stimuli (an optomotor response. Harden Jones 1963) and it has been suggested, for example, that schooling in the mouth of trawling nets is a response to a moving visual background (Kim and Wardle 2003). Such observations suggest that a moving visual background might induce an optomotor-induced schooling response in farmed salmon, thus offering a simple means of stimulating sustained exercise under high density rearing. We report here on the potential of generating a sustained swimming (schooling) response in farmed Atlantic salmon through the use of a novel lighting device that provides an apparently moving visual stimulus through sequential activation of stationary lighting columns. This non-mechanical device is relatively simple and might have value for sustainable aquaculture if a practical configuration can be found that elicits sustained exercise. Various configurations of this device were therefore tested under semi-commercial conditions, with a subsidiary aim of collecting data on growth, feed conversion ratio (FCR) and stress to identify any additional benefits.

Materials and methods

Fish and husbandry

2000 Atlantic salmon smolts (Mean \pm SE; 46.6 \pm 0.38 g mass; 170 \pm 0.35 mm FL) were transferred from the Howietoun freshwater hatchery (University of Stirling) to the Marine Environment Research Laboratory (University of Stirling, Machrihanish, Argyll) and left to acclimate for 4 weeks prior to experimentation. Fish were held under a 24 h light regime in two 7.4 m³, 3m diameter circular tanks receiving near-fully air-saturated seawater at 10 – 11 °C. Fish were fed a standard commercial salmon diet (Skretting Ltd., UK) on a maintenance ration of ~1.5% body weight d⁻¹ over the acclimation period. Water temperature varied from 11 - 14 °C (Mean \pm SE; 12.9 \pm 0.1) over the course of the 28 day growth trial outlined below.

Observation tanks and lighting system

Observations on swimming responses were performed in four identical 7.4 m³ tanks. These tanks had a central drain and received water from an inflow pipe at the side of the tank. The inflow pipe was equipped with a 90° elbow to create an anticlockwise pattern of flow. Each tank was equipped with a lighting device designed to emit a moving light pattern. Each lighting device consisted of 72 vertically aligned acrylic rods (1m long and 20mm diameter) that were equipped with a cluster of four 5mm high intensity green light emitting diodes (LEDs)(Besthongkong, Hong Kong. Wavelength = 520-525 nm; angle 20°; intensity = 30,000 mcd). Green light was selected to match the peak in wavelength sensitivity of salmon retinal pigments (Hasegawa 2006). The LEDs were mounted with a resistor on a mini circuit board and sealed in a plastic module at the top end of the acrylic rods. A series of 19 shallow 'v' shaped notches were also milled every 5cm along the length of the rods. Each acrylic rod

acted effectively as a glowing light guide but light was also intentionally refracted outwards from the notches. A mirror in a cap at the base of the acrylic rod helped to preserve light in the light guide and intensified the amount of light being emitted from the notches.

Pilot studies had already indicated that such a light system could induce sustained swimming in fish, so here different configurations were tested. The acrylic rods for each of the 4 lighting systems were aligned as a circular array in 2 different configurations. Two tanks were equipped with a device in an “outer ring configuration” where all 72 rods were spaced regularly around the inner wall of the tank. Fish in the tank were therefore active within this 3m diameter array. The remaining two tanks were equipped with a device in an “inner ring configuration” where all 72 rods were held in a 0.7 m diameter ring and positioned on 1cm blocks over the central drain in the middle of the tank. Fish in the tank were therefore active around this central array.

Customised power supplies, sequencer units and software were used to fire the LEDs sequentially in a set lighting pattern at various speeds. The lighting pattern in all four tanks was identical, based on pilot observations and consisted of a continuous 4 lights “on”: 4 lights “off” pattern which resulted in nine lighting groups and half of the lights “on” at any one time. The lighting pattern was fixed between tanks, but was set to move sequentially in a clockwise direction at different speeds according to the length of the fish being introduced. One of the tanks set in the outer ring configuration had a lighting pattern that moved one position every 30 s which was designed as a low speed control being more or less stationary i.e. 0.0 body lengths per second (BL s^{-1}). The other tank in the outer ring configuration had a lighting pattern that moved one position at a time at a speed equivalent to a salmon swimming at 1.5 BL s^{-1} when positioned 15cm from the outer wall of the tank. The remaining two inner ring configuration tanks were set to the same 1.5 BL s^{-1} speed.

Trial schedules

500 smolts were transferred at the start of the trial (5th June 2006) to each of the four 7.4 m³ tanks set with 80cm depth (water volume = 5.6 m³). Forty-five percent of these fish (n = 225 in each tank) were initially anaesthetised (0.2 ml L⁻¹ 2-phenoxy-ethanol), their mass (g) and fork length (mm) recorded and a uniquely encoded visible implant tag (Northwest Marine Technologies, WA, USA) implanted into the transparent tissue of the adipose eyelid using a specialised implant applicator (Northwest Marine Technologies, WA, USA).

Once fish were introduced to the tanks, water inflow was standardised to the lowest rate of turnover that ensured a sufficiently high level of dissolved oxygen (DO) in all tanks (>90% saturation). The anticlockwise flow of water in the tank was also standardised to a very low level (<2 cm s⁻¹ max) by adjusting the position and angle of the inflow pipe. A portable electromagnetic flow meter (Sensa SA1) was used to confirm that water flow did not differ over the course of the trials. Whilst water stream was fixed and indifferent between the four tanks at the start of the trial we did not account for any difference in flow that might have been generated through differences in swimming. DO was checked daily using an oxygen meter (Oxyguard International AS, Birkerød, Denmark).

Once the average length of the fish in the tanks was known, the lighting protocol for each of the four tanks was programmed and activated the following day. The speed of the lighting devices was only based on the body length of the fish at the start of the trial; lighting speed was not adjusted as the fish grew. This allowed at least 8 hours for the fish to acclimate to their new surroundings and to recover from the anaesthetic. Once activated, the 28 day observation period began with the tanks covered in black lightproof plastic (250 µm) to minimise external disturbance and to maintain a constant level of light (5 Lux). Feed in all four tanks was delivered continuously by a screwfeeder (Aquaculture Engineering Ltd, UK) at a rate of 4% BW d⁻¹. Tanks were cleaned on a regular basis to ensure that uneaten feed did not build up and compromise water quality.

Monitoring swimming

A CCD camera (TVCCD-24, Monacor International, Bremen) equipped with a 4mm lens was mounted above each tank for the purpose of monitoring the fish over the trial. The video signal from each of the four tanks was sampled through a Monacor quad processor (TVSP-44) and recorded for 2 min every 4 h on a DVD recorder (Panasonic DMR-E225) over the course of the trial. The speed and direction of fish swimming in the four experimental tanks was estimated from the DVD recordings over the course of the 28 day trial. Fish swimming speed in $BL s^{-1}$ was estimated from the video recordings by tracking the distance fish travelled over a multitude of frames (typically 2 - 10 seconds worth of video) and relating the distance moved (d) over time (t) to the estimated length of the fish from the snout to the tip of the tail (body length or BL) according to the formula:

$$\text{Swimming speed } (BL s^{-1}) = \left(\frac{d}{BL}\right) / t$$

Ten independent estimates of routine swimming speed were carried out each day for each tank as described above. In addition, an estimate was made of the broad direction in which the fish were swimming and a value assigned to each estimate, 1 denoting clockwise; -1 denoting anticlockwise. To examine whether there was any change in behaviour over the course of the trial, average daily swimming speed and direction were regressed over time for each tank. Values over the course of the trial were pooled to derive a total average estimate of swimming speed and direction. The camera configuration did not allow us to control for changes in swimming depth when estimating swimming speed, which added noise to the estimates. However, it was apparent that fish tended to swim at a constant depth.

Assessing physiological stress and productivity

On the 28th day of the trial a sample of blood was extracted rapidly from 19 - 21 fish (within 8 mins) in each of the four tanks. Fish were killed with a blow to the head and a sample of blood (approximately 0.2 ml) extracted rapidly by caudal

venepuncture using a heparinised syringe. Whole blood was spun at 12,000 *g* and 4 °C for 5 min and the supernatant plasma stored in either liquid N₂ or a -80°C freezer for later analysis. Plasma cortisol was measured spectrophotometrically with a microtiter plate reader (Dynatch Laboratories MRX) at 450 nm using an enzyme-linked immunoassay test kit (Adaltis EIAgen Cortisol L14003K) as described by Herbert and Steffensen (2005). All remaining fish in the tank were then killed by an overdose of anaesthetic (2-phenoxy-ethanol) followed by a blow to the head and their mass (g) and fork length (mm) recorded. Weight specific growth rate (SGR_W) over the course of the 28 day trial was calculated from the tagged fish according to the following equation:

$$SGR_W = \frac{100 \times (\ln W_2 - \ln W_1)}{T}$$

where W_1 = weight of fish (g) at the start of the experiment, W_2 = weight of fish (g) at the end of the experiment and T = duration of the experiment (days).

Length growth rate (GR_L) in mm d⁻¹ was calculated from the following equation:

$$GR_L = \frac{L_2 - L_1}{T}$$

where L_1 = length of fish (mm) at the start of the experiment, L_2 = length of fish (mm) at the end of the experiment and T = duration of the experiment (days).

The condition factor (CF) of the fish was calculated according to the following equation:

$$CF = \frac{100 \times Weight}{(length\ in\ cm)^3}$$

CF was calculated at the start and end of the trial and a change in CF value (ΔCF) derived to gauge the change in body shape over the trial. Positive ΔCF values indicate the fish grew relatively more in weight compared to length (i.e. they bulked out). A negative ΔCF value indicates fish grew relatively less in length compared to weight and the fish appeared more slender.

Feed conversion rate (FCR) was calculated according to the following formula:

$$FCR = \frac{\text{Total food fed (kg)}}{\text{Total gain in weight (kg)}}$$

Statistical analyses

To assess whether parametric or non-parametric tests would apply, normality and equal variance tests were performed on all data using Kolmogorov-Smirnov and Levene's test respectively. Linear regression analysis was performed to test whether speed and directionality of swimming changed over time. Where a significant effect of time was detected, fish behaviour data was log transformed and analysis of covariance (ANCOVA) performed to resolve differences across the four experimental groups. ANCOVAs were followed by Tukey *post-hoc* tests for specific pair-wise comparisons. Due to non-normal distributions, differences in total average swimming speed, directionality, growth, FCR and CF among the four experimental tanks were tested using Kruskal-Wallis ANOVA, followed by multiple pair-wise comparisons using the Dunn's Method. Plasma cortisol values were log-transformed and a one-way ANOVA performed to address physiological differences (stress) between fish across the four experimental tanks. This was followed by Tukey *post-hoc* tests for multiple pairwise comparisons. All analysis was performed using either STATISTICA (version 9) or Sigmastat version 2.03 with $P \leq 0.05$ assumed to denote a significant difference.

Results

Swimming speed and direction

The average swimming speed of the fish varied with configuration and differed between the four tanks (Kruskall Wallis ANOVA. $H_3 = 470.24$, $P < 0.01$)(Fig. 1a). Multiple pair-wise comparisons using the Dunn's Method revealed that swimming speed was comparable between the two outer ring configurations ($<0.5 \text{ BL s}^{-1}$) but was significantly lower than the two inner ring configurations ($1.2 - 1.5 \text{ BL s}^{-1}$)($P < 0.05$). Swimming speed was also shown to vary over time according to lighting configuration (Fig. 1b and table 1). The outer ring configurations set to speeds of 0.0 BL s^{-1} and 1.5 BL s^{-1} both yielded a significant decline in swimming speed over the course of the trial (i.e. to $<0.5 \text{ BL s}^{-1}$) while the inner ring configurations set to 1.5 BL s^{-1} resulted in a highly significant increase in mean fish swimming speed over time (i.e. from approximately 0.6 BL s^{-1} in both tanks to $\geq 1.8 \text{ BL s}^{-1}$ after 28 days)(Fig. 1b and table 1). Incorporating the effects of time into an ANCOVA test revealed that the average swimming speed of the fish depended on configuration and differed between the four tanks ($F_3 = 65.14$, $P < 0.01$). Multiple pair-wise comparisons confirmed that swimming speed was again comparable between the two outer ring configurations and slower than the two inner ring configurations ($P < 0.05$).

Table 1. Relationships between fish swimming speed (BL s^{-1}) and time in days over the course of the trial for the 4 different lighting configurations. The start and end speed of the fish on days 0 and 28 respectively is calculated from the regression.

Swim speed vs time (days)	Relationship ($x = \text{days}$, $y = \text{BL s}^{-1}$)	R^2	F	P	Starting speed (BL s^{-1})	Ending speed (BL s^{-1})
0.0 BL s^{-1} OUTER ring	$y = -0.0156x + 0.732$	0.18	5.15	<0.05	0.73	0.30
1.5 BL s^{-1} OUTER ring	$y = -0.0136x + 0.666$	0.29	9.26	<0.01	0.67	0.29
1.5 BL s^{-1} INNER ring 1	$y = 0.0428x + 0.599$	0.63	38.29	<0.01	0.60	1.80
1.5 BL s^{-1} INNER ring 2	$y = 0.0565x + 0.656$	0.72	60.21	<0.01	0.66	2.24

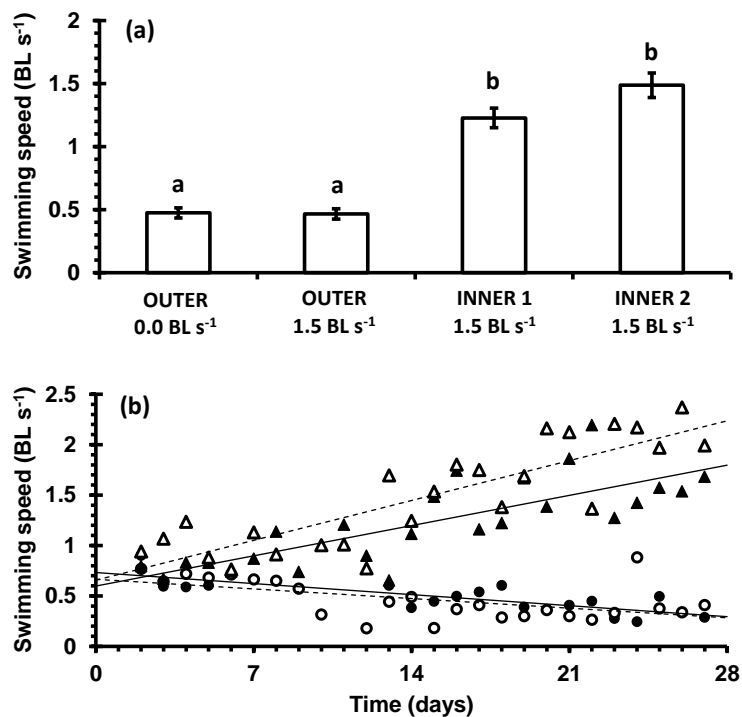


Figure 1. A) The average swimming speed of salmon (BL s^{-1}) in 4 tanks in response to 2 lighting configurations (inner vs. outer) set to move at different speeds (0.0 vs. 1.5BL s^{-1}). Data are presented as means \pm 95% confidence intervals. Data with dissimilar letters are significantly different ($P < 0.05$). B) The daily average swimming speed of salmon over the 28 day trial in response to different lighting configurations according to: 0 BL s^{-1} outer ring (closed circles), 1.5 BL s^{-1} outer ring (open circles), 1.5 BL s^{-1} inner ring 1 (closed triangles) and 1.5 BL s^{-1} inner ring 2 (open triangles). Linear regression lines are fitted to the data with further information available in Table 1. Solid regression lines refer to the 0 BL s^{-1} outer ring and the 1.5 BL s^{-1} inner ring 1 groups. Broken regression lines refer to the 1.5 BL s^{-1} outer ring and the 1.5 BL s^{-1} inner ring 2 groups.

The total average directional response of the fish also depended on configuration and differed between the four tanks (Kruskall Wallis ANOVA. $H_3 = 224.7$, $P < 0.01$)(Fig. 2a). Preference for an anticlockwise direction was weak but comparable between the two outer ring configurations (average directionality in both tanks approximately -0.16)($P < 0.05$)(Fig. 2). The directionality of fish in the two inner ring tanks also did not differ ($P > 0.05$) but they had a much greater tendency for swimming in an anticlockwise direction (-0.82 and -0.85 . $P <$

0.05)(Fig. 2). It should be noted that all moving light stimuli were configured in a clockwise direction; so the fish were swimming against the direction of the lights. Swimming direction was also found to vary over time with differences between configurations (Fig. 2b and Table 2). All fish at the start of the trial showed a slight preference for swimming with the water current in an anticlockwise direction (average directionality -0.28 to -0.64). However, over the course of the trial this preference weakened and disappeared in the 2 tanks with outer ring devices. This change in directionality over time was only significant for the outer ring 0.0 BL s⁻¹ group, though in both outer ring groups there was no directionality by day 28 (directionality 0.08 to -0.06, see Table 2). In contrast, the preference for the anti-clockwise swimming direction strengthened with time in the two inner ring groups, with almost 100% of the fish schooling in this direction by the end of the trial (see Table 2). Including the effect of time into an ANCOVA test revealed that the total average directional response of the fish did indeed depend on configuration and differed between the four tanks ($F_3 = 60.11$, $P < 0.01$).

Table 2. Relationships between fish swimming direction and time in days over the course of the trial for the 4 different lighting configurations. The start and end directionality of the fish on days 0 and 28 respectively is calculated from the regression. 1= 100% clockwise; -1= 100% anticlockwise; 0 = no directionality.

Directionality vs time (days)	Relationship ($x = \text{days}$, $y = \text{BL s}^{-1}$)	R ²	F	P	Starting directionality	Ending directionality
0.0 BL s ⁻¹ OUTER ring	$y = 0.0219x - 0.531$	0.34	8.72	<0.01	-0.53	0.08
1.5 BL s ⁻¹ OUTER ring	$y = 0.00774x - 0.277$	0.06	1.46	ns	-0.28	-0.06
1.5 BL s ⁻¹ INNER ring 1	$y = -0.0146x - 0.637$	0.28	8.97	<0.01	-0.64	-1.05
1.5 BL s ⁻¹ INNER ring 2	$y = -0.0214x - 0.509$	0.59	33.71	<0.01	-0.51	-1.11

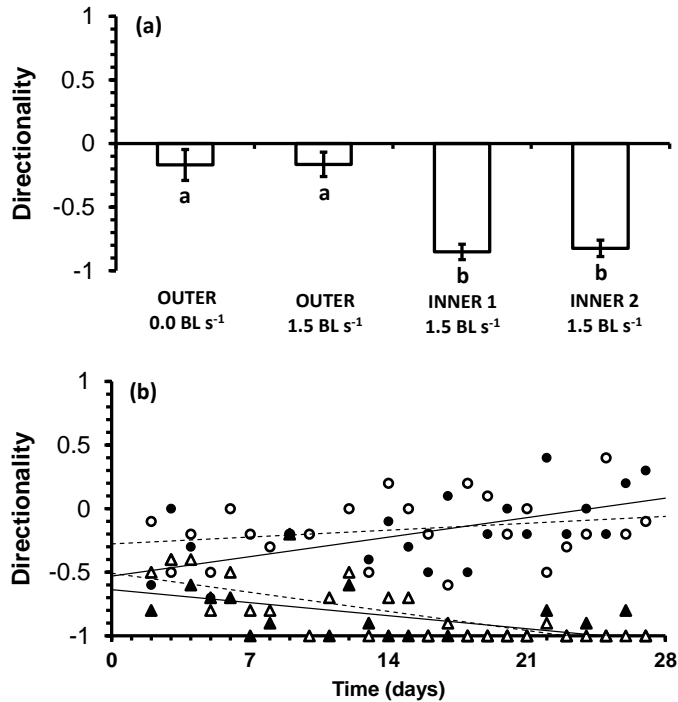


Figure 2. A) The average directional response of salmon in 4 tanks in response to 2 lighting configurations (inner vs. outer) set to move at different speeds (0.0 vs. 1.5 BL s⁻¹). 1= 100% clockwise; -1= 100% anticlockwise; 0 = no directionality. Data are presented as means \pm 95% confidence intervals. Data with dissimilar letters are significantly different ($P < 0.05$). B) The daily average directional response of salmon over the 28 day trial in response to different lighting configurations according to: 0 BL s⁻¹ outer ring (closed circles), 1.5 BL s⁻¹ outer ring (open circles), 1.5 BL s⁻¹ inner ring 1 (closed triangles) and 1.5 BL s⁻¹ inner ring 2 (open triangles). Linear regression lines are fitted to the data with further information available in Table 2. Solid regression lines refer to the 0 BL.s⁻¹ outer ring and the 1.5 BL s⁻¹ inner ring 1 groups. Broken regression lines refer to the 1.5 BL s⁻¹ outer ring and the 1.5 BL s⁻¹ inner ring 2 groups.

Fish in the inner ring groups responded positively to the lights in terms of both speed and direction and therefore swam approx 15 - 30cm from the side of the wall due to centrifugal forces forcing them to the sides of the tank. In contrast, fish exposed to the outer ring stimuli did not exhibit a swimming response and therefore showed a more even distribution across the diameter of the tank with little directionality (Fig. 2).

Physiological stress and productivity

Plasma cortisol concentrations were significantly different between the 4 groups (ANOVA. $F_{3,82} = 2.714$, $P = 0.05$)(Fig.3). However, *post-hoc* analyses revealed a significant difference only between the 0.0 BL s^{-1} outer ring and the 1st 1.5 BL s^{-1} inner ring group ($P < 0.05$), with the average value for fish on inner ring configuration being 56% lower.

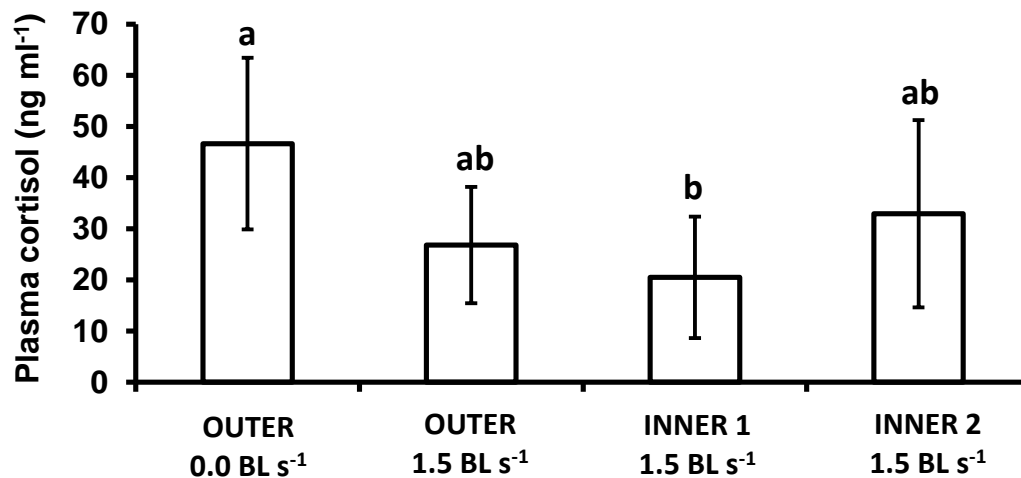


Figure 3. Average plasma cortisol levels (ng ml^{-1}) sampled from salmon in 4 tanks with 2 lighting configurations (inner vs. outer) set to move at different speeds (0.0 vs. 1.5 BL s^{-1}). Data are means \pm 95% confidence intervals. Data with dissimilar letters are significantly different ($P < 0.05$).

Average fork length increased from $171 \pm 0.3 \text{ mm}$ to $187 \pm 0.5 \text{ mm}$ over the course of the trial, whilst total average weight increased from $46.6 \pm 0.4 \text{ g}$ to $62.2 \pm 0.5 \text{ g}$. Fish biomass therefore increased from $3.8 - 4.5 \text{ kg m}^{-3}$ to $4.6 - 6.0 \text{ kg m}^{-3}$ by the end of the trial. Over this period there were significant differences between tanks in SGR_W (Kruskall Wallis ANOVA. $H_3 = 22.35$, $P < 0.01$), GR_L (Kruskall Wallis ANOVA. $H_3 = 95.72$, $P < 0.01$) and ΔCF (Kruskall Wallis ANOVA. $H_3 = 14.95$, $P < 0.01$). More detailed analysis generally revealed that fish in the 2 inner ring tanks grew significantly faster than fish in the 0.0 BL s^{-1} outer ring tank in terms of both weight and length ($P < 0.05$)(Table 3). Growth in the outer 1.5 BL s^{-1}

¹ tank was generally intermediate between these groups and only differed clearly from both the 0.0 BL s⁻¹ outer ring group and the 2 inner ring groups in terms of GR_L (Table 3). Interestingly, fish in the 1st 1.5 BL s⁻¹ inner ring group assumed a more slender body shape (i.e. reduced CF) whilst maintaining one of the fastest rates of weight specific growth (Table 3). The slender body shape was clearly visible to the human eye at the end of the trial. At the same time, the proportion of fish losing weight was markedly lower in the 2 inner ring tanks (Table 3).

Table 3. Differences in the productivity (growth and FCR) of fish in 4 tanks in response to 2 lighting configurations (inner vs. outer) set to move at different speeds (0.0 vs. 1.5 BL s⁻¹). Data are presented as means ± SE. Data with dissimilar letters are significantly different (P < 0.05).

Lighting configuration and speed	SGR _w (% d ⁻¹)	GR _L (mm d ⁻¹)	Δ CF	FCR	% fish losing weight
0.0 BL s ⁻¹ OUTER ring	0.79 ± 0.05 ^a	0.45 ± 0.02 ^a	0.007 ± 0.005 ^a	0.88	13.2
1.5 BL s ⁻¹ OUTER ring	0.94 ± 0.04 ^{ab}	0.53 ± 0.02 ^b	0.012 ± 0.005 ^a	0.77	10.6
1.5 BL s ⁻¹ INNER ring 1	1.05 ± 0.03 ^b	0.67 ± 0.01 ^c	-0.013 ± 0.004 ^b	0.71	3.4
1.5 BL s ⁻¹ INNER ring 2	1.08 ± 0.03 ^b	0.65 ± 0.01 ^c	0.0 ± 0.004 ^{ab}	0.68	2.0

All tanks had FCRs <0.9 indicating extremely good rates of feed conversion, compared to the stock tank at Machrihanish, which was 0.98 over this period (Dr. William Roy pers comm). Sample sizes did not permit statistical analysis, but the FCRs of the two inner ring tanks were very low at 0.68 - 0.71, representing a 19-22% improvement in food conversion efficiency compared the 0.0 BL s⁻¹ outer ring group (FCR = 0.88). The 1.5 BL s⁻¹ outer ring had an FCR of 0.77; 12% more efficient than the 0.0 BL s⁻¹ outer ring group. No mortality, infection or disease was observed through the experiment.

Discussion

Swimming speed and direction

An inner ring light configuration was far more effective at inducing sustained swimming by Atlantic salmon than one in which lights are placed on the outer wall of tanks. This is fortunate for ongoing technology development, since, compared to the outer ring configuration, the inner ring lends itself better to commercial scale-up. It would be relatively simple to deploy an inner ring device in the centre of commercial seacages or large tanks. In contrast, lights aligned around the outer perimeter of our tanks did not elicit sustained exercise in the current trial and this configuration would certainly not be practical to deploy with respect to routine farming practice in commercial systems. Further developments of this concept therefore look promising for the sustainability of salmon aquaculture. Further research may also reveal that fish swimming technologies of this type are applicable for the farming of alternative fish species which would otherwise not swim at optimal speeds under low flow conditions.

The speed and directional consistency attained by salmon swimming around the inner ring devices was impressive. At the end of the trial all fish were observed schooling on a sustained basis in an anti-clockwise direction at speeds in the region of 1.8 - 2.24 BL s⁻¹ (Table 1). This was not an immediate response, linear increases in both speed and directionality appearing over time. By comparison fish failed to initiate a positive swimming response to light from the outer ring configuration (both stationary and moving) with swimming speed and directionality weakening over time (Table 1). Multiple lighting groups which are visible to the fish at all times are probably confusing and certainly appear to disrupt schooling and sustained swimming behaviour.

So what are the mechanisms that generate sustained swimming with increasing speed and directionality over time in the inner ring tanks? The increased swimming is not simply a response to light, since light output intensity was standardized between all tanks. In terms of stimulating swimming, the innate

optomotor response that enables fish to stabilize their position with respect to moving visual backgrounds could be involved (Harden Jones 1963; Veselov et al. 1998; Kim and Wardle 2003). Indeed, most species of fish tested in these studies, including Atlantic salmon, saithe, mackerel, flatfish and pike exhibit strong optomotor responses. There are two moving backgrounds, however, to which fish in the current experiment could have orientated and swam as a way of stabilizing their position in the water column. The first is the moving light pattern of the device itself and the second is the visual background of schooling conspecifics. The fact that the salmon swam in the opposite direction to the lights (i.e. anticlockwise vs. clockwise) suggest that they were not showing a simple, direct optomotor response to the lights. Instead, it seems that they stabilized their position with respect to conspecifics and may have therefore shown a schooling optomotor reaction (Shaw and Tucker 1965) as an indirect response to the lights. This is the first study of its kind, however, and further studies are required to clarify the exact behavioural nature of the observed response to the apparently-moving lights. The observed increase in swimming speed over time could be the result of progressive exercise-training allowing enhanced swimming performance and progressively faster speeds to be attained.

Associated benefits

The results presented here are generally consistent with published data on the benefits of sustained exercise at optimal speeds in active species of fish, including the Atlantic salmon. For example, in response to the inner ring devices, our fish swam at an average speed of 1.2 - 1.5 BL s⁻¹ and may have shown considerably greater rates of weight-specific and length growth (Totland et al. 1987; Houlihan and Laurent 1987; Christiansen et al. 1989; Christiansen et al. 1992; Jørgensen and Jobling 1993; Young and Cech 1993; Yogata and Oku 2000), improved FCR (Christiansen et al. 1992; Jørgensen and Jobling 1993; Yogata and Oku 2000) and some evidence of reduced basal levels of plasma cortisol (Boesgaard et al. 1993)(Table 3). All these benefits could improve fish

farming practice by lowering the costs and environmental impacts of feed and boosting general fish welfare via lowered stress, assuming the latter is achieved adequately through lowered plasma cortisol levels (Huntingford et al. 2006). The more slender body shape of exercised fish may also improve the aesthetic quality and value of fish. Overall productivity could also be improved with fewer runts and more fish going on to harvest (Table 3). There are apparently few known negative effects of sustained moderate exercise for the Atlantic salmon (Totland et al. 1987; Boesgaard et al. 1993; Jørgensen and Jobling 1993; Davison 1997) and the results appear to corroborate the view that exercise could help improve the long-term sustainability of salmon aquaculture. This would be achieved by meeting the multiple demands of the industry in terms of improved productivity, quality and welfare.

The growth benefits for smolts swimming at an average speed of 1.2 - 1.5 BL s⁻¹ in the inner ring tanks are comparable to the growth improvements of salmonids swimming in currents at 1.0 - 2.0 BL s⁻¹ (Totland et al. 1987; Houlihan and Laurent 1987; Christiansen et al. 1989; Christiansen and Jobling 1990; Jørgensen and Jobling 1993). While it might be counter-intuitive for growth to be enhanced at a time of high energetic expenditure, the optimal least cost speed of salmon does appear to reside in the vicinity of 1.0 - 1.7 BL s⁻¹ depending on body size and temperatures (Grøttum and Sigholt 1998; Lee et al. 2003; Deitch et al. 2006). Whilst this range is quite wide, the energetics model of Grøttum and Sigholt (1998) did allow us to compute U_{opt} for a 60 g Atlantic salmon at 12.9 °C with an estimated value of 1.7 BL s⁻¹, making the higher values more relevant for this discussion. There is therefore considerable overlap between energetic U_{opt} and the speeds at which *S. salar* grew fast, implying that the metabolic costs of growth and exercise can be accommodated at the same time. It should be noted, however, by the end of our trial our salmon were swimming at speeds in excess of U_{opt} (i.e. 1.8 - 2.25 BL s⁻¹). On that note it would be interesting to test whether long-term voluntary exercise could feasibly raise U_{opt} , allowing growth benefits at faster speeds. Another interesting issue to emerge from these data is the difference in rate of growth in length between the two outer ring configurations in

the absence of any difference in swimming. This may be an effect of the lights per se, but requires further investigation.

Conclusions

This study has shown that an apparently-moving light stimulus can be used to induce sustained swimming in farmed Atlantic salmon and that the inner ring light system is far more effective than the outer ring configuration, with concomitant gains in growth, feed conversion efficiency and reduced stress. However, the study has also shown that we clearly have much to learn both about the behavioural mechanisms that underlie this response and about how the device might operate under a wider range of conditions. The wealth of benefits arising from sustained exercise at an optimal speed (Totland et al. 1987; Jørgensen and Jobling 1993; Davison 1997) provide an excellent fish farming strategy and future developments in novel fish swimming technologies may prove to be beneficial for the sustainability of farmed fish culture.

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