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Tolerance to fluctuating currents in farmed Atlantic salmon: a novel method to simulate offshore wave effects in the laboratory

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ABSTRACT: To ensure acceptable animal welfare in emerging offshore Atlantic salmon aquaculture, it is crucial to understand the biological limits of the fish. Much work has been done on the effects of water currents, but few studies exist on waves, owing to logistical limitations. The purpose of this study was therefore to establish a method to replicate wave-like fluctuating water currents in the laboratory and quantify tolerance limits in salmon. To accomplish this, a swim tunnel system was modified so that current speeds could be programmed to automatically alternate between minimum and peak speeds of a desired magnitude and interval. The critical swimming speed (U_{crit}) was subsequently measured in salmon of ~800 g as a baseline from which standardized tests of fluctuating currents could be prescribed. Fluctuating current trials were then performed using minimum speeds of 20% U_{crit} and peak speeds of 80, 100, 120, and 140% U_{crit}, and cycles of 0.5, 1, and 2 min. Fish were tested for 4 h or until they fatigued. All fish at 80 and 100% U_{crit} endured 4 h of fluctuating currents. However, at 120% U_{crit}, only 17% completed the test, and at 140% U_{crit}, all fish became fatigued within 1.5 h, thus defining acute limits to fluctuating peak speeds. Wave interval did not affect fatigue times significantly. In conclusion, a novel method is introduced here to assess tolerances to various wave-like environments, showing that salmon can endure ~20% higher peak speeds in dynamic fluctuating currents when compared to known swimming capacities at constant speeds.

KEY WORDS: Critical swimming speed · Exposed aquaculture · Fatigue · Fish welfare · *Salmo salar* · Sustained swimming

1. INTRODUCTION

The Atlantic salmon (*Salmo salar*) aquaculture industry is facing major sustainability obstacles, most notably owing to the spread of sea lice, escapees interbreeding with wild populations, and eutrophication of local environments (Glover et al. 2017, Olaussen 2018, Dempster et al. 2021, Vollset et al. 2021). In Norway, which is the largest producer of farmed Atlantic salmon, this has led to enforced restrictions by the government on further expanding production when using traditional sheltered fjord sites along the coastline (Sjømat Norge 2021, Regjeringen 2021). Since sustainability obstacles in conventional salmon aquaculture practices are unlikely to be solved in the foreseeable future, new sites either on land or at sea are required to further increase production capacities (Bjelland et al. 2015). Therefore, a major trend in the industry and its regulation is the development of methods, technology, and governmental licensing so that salmon can be farmed at new locations offshore (Morro et al. 2022, Watson et al. 2022). Moving production offshore away from coastal areas could ameliorate key sustainability concerns

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such as local eutrophication minimize transmission of pathogens and parasites, while also reducing conflicts of interests with other coastal activities (Holmer 2010, Salama & Murray 2011, Bjelland et al. 2015). However, going further off the coast will expose new farm sites to occasionally harsher weather conditions which include powerful waves and strong water currents. This forces additional requirements upon farm structures and logistics, and moreover raises important questions about fish welfare regarding whether Atlantic salmon are able to thrive in these new high-energy environments (Johansson et al. 2014, Hvas et al. 2021a).

The concern for fish welfare in aquaculture has been receiving more attention in recent years owing to the realization by the industry that prioritizing fish welfare aligns with lower mortality rates, fewer health issues, and improved appetite and growth, as well as a more positive reputation among consumers (Noble et al. 2018, Kristiansen et al. 2020). In offshore farm environments, potential novel welfare threats are powerful waves and strong water currents. To facilitate responsible practices, it is therefore necessary to establish adequate welfare guidelines based on the biological limits of the fish to any environmental extreme they may encounter during a production cycle. So far, the focus has mainly been on defining tolerance limits for strong water currents at various time scales (Solstorm et al. 2015, Hvas et al. 2021a,b). The general conclusion was that Atlantic salmon is a powerful sustained swimmer and likely will be able to thrive at offshore aquaculture sites, considering ocean survey data of water currents at candidate locations (Jónsdóttir et al. 2019, Hvas et al. 2021a).

The impact of waves on farmed Atlantic salmon has rarely been studied and is mostly limited to field observations on the Faroe Islands (Dam 2015, Johannesen et al. 2020, 2022). There it has been shown that waves may temporarily disrupt group behaviors in sea cages, causing more chaotic states, and possibly more collisions, especially in darkness. While welfare was slightly reduced after periods with stormy conditions, behavioral effects depend on the time of day owing to diurnal changes in positional preference within the water column; moreover, less space becomes available for the fish owing to sea cage deformations. Although these sites certainly are exposed to rough weather conditions, they are situated near the coast in relatively shallow waters and may not fully represent conditions envisioned at true offshore sites with depths typically exceeding 100 m. Furthermore, they do not provide a quantifiable tolerance limit for wave effects that can be applied as fish welfare guidelines. This highlights a methodological issue, as it is very difficult to experimentally study the full impact of powerful ocean waves on fish coping ability in a laboratory setting; furthermore, appropriate open ocean aquaculture sites are not yet available for field observations. In contrast, the effects of strong water currents have so far been thoroughly studied experimentally in the laboratory with swim tunnel systems or other tank setups where fish are exposed to various flow conditions of interest (Solstorm et al. 2015, Hvas et al. 2021a, McKenzie et al. 2021).

Different types of ocean waves exist, with the most common being surface waves generated by winds (Wright et al. 1999). Owing to their origin at the surface layer, the hydrodynamic forces of wave movements diminish with increasing depth down the water column (Wright et al. 1999). Farmed salmon in a wave-exposed sea cage may thereby behaviorally avoid most of the wave forces in deeper sea cage structures, as was occasionally observed by Johannesen et al. (2020). Contrary to water currents, waves do not cause much net transport of water particles forward, although wave shapes propagate across the surface. Instead, waves are characterized by peaks and bottoms where water particles will be moved up and down, forward and back, thus creating circular movement patterns that signify 1 wave period. Depending on the size of the wave, a wave period typically lasts between 1 and 30 s (Wright et al. 1999, Albretsen et al. 2019). Furthermore, waves are often irregular, including variations in shape, height, length, and speed of propagation, while the distance to the ocean floor also influences waves, where deeper waters generally result in larger waves (Albretsen et al. 2019).

Considering the hydrodynamic environment Atlantic salmon would experience in an offshore sea cage exposed to large ocean waves, it may be viewed as a fluctuating water current going back and forth at a frequency and speed defined by the wave period and its magnitude. These fluctuating water currents would present a different kind of challenge for the fish compared to constant current speeds, owing to the fish needing to adjust swimming efforts dynamically in response to the wave pattern for it to hold position within the sea cage and to avoid colliding with the net wall and conspecifics. More specifically, swimming efforts will consist of alternating between accelerating and decelerating swimming speeds. By deconstructing wave effects into a fluctuating water current and leaving out the vertical component, one could envision smaller-scaled laboratory-based tests that would allow for studying the effects of dynamic wave-like environments on fish. Such work has previously been carried out on various smaller-sized coral reef fishes, where the aim was to characterize the metabolic cost of swimming and turning in waves and unsteady water flows, and moreover, whether morphology and swimming mode reflect species-specific adaptations to shallow wave-exposed reef habitats (Roche et al. 2014, Marcoux & Korsmeyer 2019, Schakmann et al. 2020, Schakmann & Korsmeyer 2023). In the case of larger-sized farmed Atlantic salmon exposed to waves, the principal concern is to establish a measure of tolerance limit akin to the critical swimming speed (U_{crit}) for constant water currents (e.g. Remen et al. 2016). Due to differing purposes, none of the studies on coral reef fish attempted to simulate waves strong enough to inflict physiological exhaustion.

The purpose of the present study was first to establish a method where wave-like fluctuating water currents could be replicated in the laboratory with peak magnitudes well above the aerobic swimming limit of Atlantic salmon (e.g. Hvas et al. 2021b). Secondly, this method was used on live fish, starting with establishing the mean U_{crit} of a cohort to provide a baseline from which relevant fluctuating current regimes could be prescribed. Swim trials with fluctuating water currents were then performed using minimum speeds of 20% U_{crit} and peak speeds of 80, 100, 120, and 140% U_{crit}, and cycles of 0.5, 1, and 2 min, where fish were tested for 4 h or until they became fatigued. These test regimes can be described as a unilateral wave surge scenario with sinusoidal variations in water flow in a single direction around a constant mean, similar to the approach used by Roche et al. (2014), but admittedly less realistic than providing an alternating flow in opposite directions as accomplished by others (e.g. Marcoux & Korsmeyer 2019, Schakmann et al. 2020). However, it is presumably not feasible to build similar setups upscaled to test larger-sized salmon until exhaustion.

It was hypothesized that repeatedly having to accelerate swimming speeds would be associated with a significant anaerobic burden, causing an accumulating deficit to homeostasis including lactate buildup, which eventually would result in physiological exhaustion. Owing to the presumed strenuousness of repeated swimming accelerations, the peak speed limit that would result in imminent fatigue in fluctuating current regimes was predicted to be lower than the established threshold for sustained aerobic swimming in constant current regimes, which previously has been shown to be 80–85% of the U_{crit} in Atlantic salmon (Hvas & Oppedal 2017, Hvas et al. 2021b).

2. MATERIALS AND METHODS

2.1. Fish husbandry

Cultured Atlantic salmon post-smolts (Aquagen) produced on site were maintained in 3 large circular holding tanks at the Matre Research Station, Institute of Marine Research in Norway. Each holding tank was 3 m in diameter and contained a water volume of 5.3 m^3. Each holding tank was supplied with filtered, aerated, and UV-C treated full-strength seawater of 34 ppt and 9°C at a constant flow-through of 130 l min^{-1}. This arrangement ensured a constant temperature, adequate oxygen conditions above 80% saturation at all times, and automatic removal of waste products such as carbon dioxide and ammonia.

At the time of transfer to the holding tanks approximately 1 mo prior to the experimental trials, the fish weighed ~430 g, and 150 fish were allocated into each tank, providing an appropriate stocking density of ~12.3 kg m^{-3}. Fish were subjected to a 12:12 h light:dark photoperiod between 08:00 and 20:00 h and fed in excess daily with standard commercial feed (Skretting, 4.5 mm pellet size) from automatic feeder systems.

The experimental trials were performed between September and November 2022 following ethical approval by the Norwegian Food Safety Authorities for the use of animals in scientific research (permit identification number 29323).

2.2. Swim tunnel system

A large custom-built Brett-type swim tunnel system was used to expose Atlantic salmon to different water current regimes. This setup and its technical specification were previously described by Remen et al. (2016). To summarize, the elliptical shaped tunnel (1905 l) was constructed with polypropylene pipes with an internal diameter of 36 cm and a swim section of 248 cm, providing an available volume of 252 l for the fish. A motor-driven propeller (Flygt 4630, 11° propeller blade, Xylem Water Solutions Norge) was mounted inside the tunnel opposite the swim section to generate the desired water flows. To minimize turbulence and facilitate approximately laminar flow conditions, the water first entered a resting section with a larger internal diameter and was then forced through a honeycomb section with cell diameters of 5 mm and a reduction cone before entering the swim section upstream. At the rear of the swim section, the top opening was partially removable so that fish could be transferred in and out of the tunnel between trials. A rear grid was located downstream of the swim section and behind it a camera was placed so that the fish could be observed remotely. Water from the same source as used for the fish holding tanks was supplied into the tunnel at the opposite end downstream of the motor via an adjustable inlet. A constant moderate exchange flow was provided during swim trials to ensure a stable temperature and normoxia, similar to the holding tanks.

2.3. Automation of motor controls and preliminary tests with fluctuating currents

To provide wave-like fluctuating water currents in the swim tunnel with defined peaks, bottoms, and intervals for prolonged test periods, it was necessary to automate changes in motor output via a programmable interface. For this study, motor controls were therefore updated with a programmable logic controller (PLC) that was installed and delivered by Xylem Water Solutions Norway in accordance with its requested purpose. The PLC then allowed a fixed low and high motor output in revolutions per minute (RPM) to be set together with a time interval, whereafter propeller speed would fluctuate up and down as prescribed automatically.

The RPM of the motor was thoroughly calibrated with a flow meter (Höntzsch Flow Measuring Technology) that was fixated towards the back of the swim section in the middle of the cross-sectional area so that the magnitude of the generated water current speeds could be known. Furthermore, measurements of the flow meter were logged every 3 s, which allowed for visualizing fluctuating current regime profiles via a computer program (Software UCOM for Configuring Höntzsch Transducers) during a series of preliminary tests before running trials with fish in the swim tunnel.

Since the water flow now would be fluctuating between high and low current speeds, the frequency converter's acceleration time needed to be measured to ensure that the decided rotation frequency that equaled a specific current speed was reached within a desired number of seconds. Based on protocol-specific acceleration times, this allowed for peak speeds to be reached just before the 'high-speed interval' ended whereafter the current speed started to decrease. Likewise, the lowest speed was reached just before the 'low-speed interval' ended. As such, with considerations for acceleration times at various flow speeds and interval, it was finally possible to create automatic fluctuating current speeds of a desired magnitude and periodicity.

2.4. U_{crit} protocol

To obtain a baseline of swimming capacities in the Atlantic salmon allocated to the present study, the U_{crit} of a representative subsample was measured. U_{crit} is a standardized test of the prolonged swimming performance in fish where protocols consist of incrementally ramping up flow speeds until fatigue is reached (Brett 1964, Plaut 2001). In the latter part of the test, fish will therefore be required to use both aerobic and anaerobic metabolism, and swimming efforts can only be maintained for a limited amount of time before exhaustion sets in.

The day before a swim trial, 6 fish were randomly netted from a holding tank and quickly transferred into the swim tunnel where they acclimatized overnight at a low flow speed of 15 cm s^{-1}. Six fish per swim trial were chosen based on their size to obtain a relevant stocking density of approximately 20 kg m^{-3} (Turnbull et al. 2005). In order to reduce acute handling stress from being netted and briefly air-exposed during movement of the fish, the swim tunnel system was located in the same room as the holding tank.

The next morning, the swim trial started and consisted of increasing current speeds by 15 cm s^{-1} every 30 min until all the fish had become fatigued. Fatigue was defined when a fish was no longer able to maintain consistent swimming against the current, even followed by touch from the experimenter's hand. Fatigued fish would then end up being stuck against the rear grid, whereafter they were removed and euthanized with a quick blow to the head. Elapsed time was recorded, and fork length and weight were measured. The swim trial continued until all fish were fatigued. Three replicated U_{crit} trials were performed using fish from a novel holding tank each time, providing 18 individual U_{crit} measurements in total.

2.5. Fluctuating current speed protocols

Peak and bottom speeds in the fluctuating current protocols were based on the mean U_{crit} obtained in the preceding trials. As such, in all trials, bottom speeds were 20% of the U_{crit}, while 4 different peak speeds were tested, consisting of 80, 100, 120, and 140% of the U_{crit} and a periodicity of 1 min (Fig. 1A). Furthermore, 3 different wave periods of 0.5, 1, and 2 min were tested with peak speeds of 120% U_{crit} (Fig. 1B).

Similar to the U_{crit} trial, 6 random fish were netted from a holding tank and left to acclimatize in the swim tunnel overnight at 15 cm s^{-1}. The following morning, fluctuating swim trials were initiated and started with

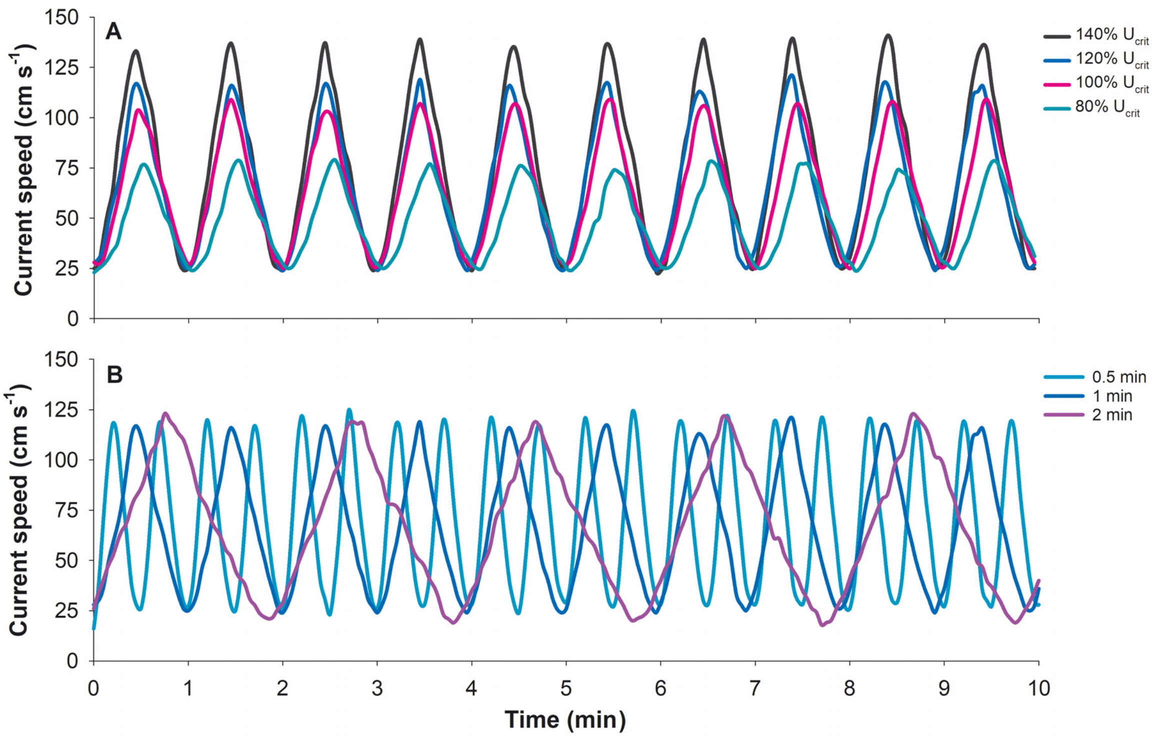

Fig. 1. Representative visualization of measured fluctuating current regime from the experimental trials. (A) Different peak currents with a periodicity of 1 min. (B) Similar peak currents (120% U_{crit}) with different periodicities. Swim trials with these water current profiles continued for 4 h or until the fish became fatigued. U_{crit}: critical swimming speed

a warm-up period where current speeds were increased by 15 cm s^{-1} every 5 min until a subsequent increase would exceed the prescribed peak speed. Thereafter, water currents were set to fluctuate automatically. Trials then continued for 4 h or until the fish became fatigued, as described for the U_{crit} trials. Fish that endured 4 h in the swim tunnel were noted to have completed the test. Afterwards, all fish were euthanized, and weight and fork length were recorded.

Three replicate trials were performed for each treatment protocol. Hence, with the inclusion of the U_{crit} trials, a total of 126 fish were tested in the swim tunnel system for the present study.

2.7. Calculations

U_{crit} was calculated according to Brett (1964) as:

$$U_{crit} = U_f + \frac{t_f U_i}{t_i} \quad (1)$$

where U_f is the highest completed current speed (cm s^{-1}), t_f is the time endured on the final speed before reaching fatigue (min), U_i is the velocity increment (15 cm s^{-1}), and t_i is the time increment interval (30 min). Owing to the larger cross-sectional area of the swim tunnel relative to the fish, solid blocking effects were not corrected for, as the effect would have been minimal (Bell & Terhune 1970).

As a standardized morphometric parameter, the condition factor of each fish was calculated as 100 × weight (g)/fork length (cm)^3 (Nash et al. 2006).

2.8. Statistics

A 1-way ANOVA with a subsequent Tukey's honest significant difference (HSD) post hoc test was used to test for differences in size parameters between the treatment groups after having confirmed normality and equal variance with the Shapiro-Wilk test and the Brown-Forsythe test, respectively. Pearson correlation tests and linear regressions were used to assess relationships between measured parameters of interest, such as U_{crit} versus size parameters, and relative peak swimming speed versus fatigue time, in fish that became fatigued. A 1-way ANOVA was used to test whether wave periods affected fatigue times following log transformation of data to adhere to test assumptions, and a Mann-Whitney rank sum test was used to compare time of fatigue between treatment groups with different peak speeds. Data analyses were performed in SigmaPlot (v.14.5, Systat Software). p-values below 0.05 were considered significant, and data are reported as mean ± SEM unless specified otherwise.

3. RESULTS

Across treatments, the weight, fork length, and condition factor of the fish tested were 837 ± 14 g, 41.1 ± 0.2 cm, and 1.19 ± 0.01, respectively. The size parameters for each treatment group are summarized in Table 1. The U_{crit} group and the 80% U_{crit} fluctuating current group had significantly lower weights, fork lengths, and condition factors compared to the 140% U_{crit} fluctuating current group (1-way ANOVA, $p < 0.05$). These size disparities are explained by the order of the trials, as approximately 5 wk had passed between them, allowing the fish to grow slightly. All other comparisons in size parameters between groups were not statistically different.

The U_{crit} was 94.5 ± 1.6 cm s^{-1}, which corresponded to 2.40 ± 0.05 body lengths s^{-1}. One fish was removed from the dataset as it displayed an obvious compromised swimming ability (>2 SD from the mean), likely caused by abdominal skin wounds that were first discovered afterwards. The U_{crit} expressed in cm s^{-1} was not correlated with weight (Pearson, correlation coefficient = 0.077, $p = 0.77$). However, when expressed as body lengths s^{-1}, the correlations were significant (Pearson, correlation coefficient = −0.53, $p = 0.031$) (Fig. 2).

Based on the measured U_{crit}, the derived peak current speeds in the subsequent fluctuating current trials of 80, 100, 120, and 140% U_{crit} were defined as 76, 95, 114, and 133 cm s^{-1}, respectively, while the minimum speed of 20% U_{crit} used for all treatments corresponded to 19 cm s^{-1}. Furthermore, during the fluctuating swim trials, the average measured current speeds experienced by the fish over time were 49, 63, 68, and 75 cm s^{-1} in the 80, 100, 120, and 140% U_{crit} peak groups, respectively, when using a peridiocity of 1 min. Additionally, when using other periodicities at 120% U_{crit} peak speeds, the average experienced current speeds remained similar (Table 1).

The general behavior of the fish inside the swim tunnel when subjected to fluctuating currents was found to be appropriate as they adjusted swimming efforts accordingly in response to the cyclical changes in flow speeds. However, it was observed that early in the trial, swimming appeared more chaotic, with some collisions between fish, whereafter group behavior became more orderly after having experienced a handful of cycles, especially at the lower peak speeds of 80 and 100% U_{crit}. At the higher peak speeds, swimming remained more chaotic. During the intermittent periods of minimum speeds, fish were often observed to briefly rest at the bottom of the tunnel. Fish that were approaching fatigue would first swim less steadily and eventually they were unable to accelerate fully during peak periods, leading them to get stuck at the rear end of the swim tunnel.

In the fluctuating current trials with a periodicity of 1 min, all fish completed the 4 h test when using peak speeds of 80 and 100% U_{crit}. However, at peak speeds of 120% U_{crit}, only 4 out of 18 fish endured 4 h, and at peaks of 140% U_{crit}, all fish became fatigued within 1.5 h, with a mean fatigue time of 51 ± 4 min (Fig. 3). For those fish that became fatigued, time of fatigue was neither significantly correlated with relative swimming speeds in the 120% or in the 140% U_{crit} peak groups (Pearson, $p > 0.05$ in both). However, all fatigued fish across treatment groups showed a significant negative correlation between relative swimming speed and time of fatigue (Pearson, correlation coefficient = −0.579,

Table 1. Treatment protocols, current speeds experienced by the fish, and their size parameters in the different groups. Percentage of the critical swimming speed (U_{crit}) refers to the defined peak speed in fluctuating current trials; time in seconds refers to the interval between peaks. Different superscript letters indicate statistical differences between groups in size parameters (1-way ANOVA, $p < 0.05$), n = 18, and data are mean ± SEM. NA: not applicable

Treatment	Peak speed (cm^{-1})	Minimum speed (cm s^{-1})	Average speed (cm s^{-1})	Weight (g)	Fork length (cm)	Condition factor
U_{crit} test	NA	NA	NA	719 ± 33^{a}	39.8 ± 0.5^{a}	1.13 ± 0.02^{a}
80% U_{crit}, 1 min	79	23	49	767 ± 35^{a}	40.5 ± 0.6^{a}	1.14 ± 0.02^{a}
100% U_{crit}, 1 min	109	25	63	831 ± 24^{ab}	41.1 ± 0.4^{ab}	1.19 ± 0.02^{ab}
120% U_{crit}, 1 min	120	24	67	868 ± 37^{ab}	41.6 ± 0.4^{ab}	1.20 ± 0.02^{ab}
140% U_{crit}, 1 min	141	23	75	951 ± 34^{b}	42.3 ± 0.4^{b}	1.25 ± 0.01^{b}
120% U_{crit}, 0.5 min	125	23	68	864 ± 36^{ab}	41.4 ± 0.5^{ab}	1.20 ± 0.02^{ab}
120% U_{crit}, 2 min	124	19	68	853 ± 30^{ab}	41.2 ± 0.5^{ab}	1.21 ± 0.02^{ab}

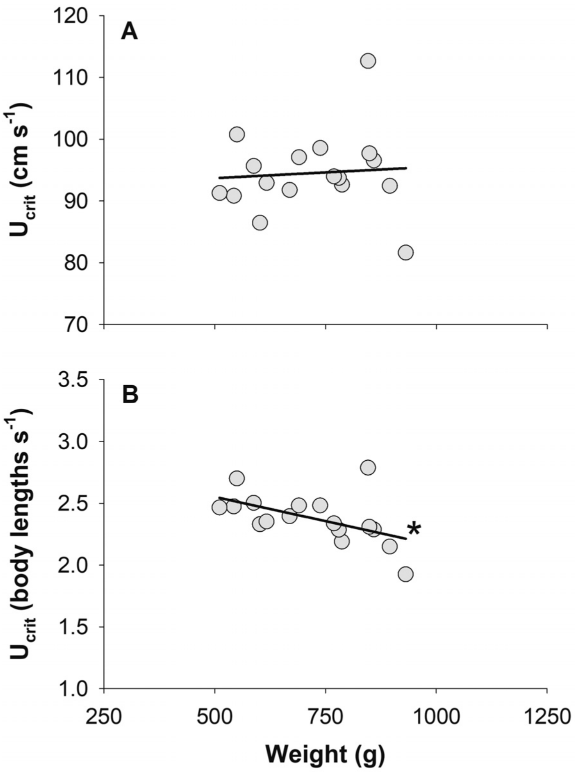

Fig. 2. Critical swimming speed (U_{crit}) expressed in (A) absolute and (B) relative units versus body mass. Lines are linear regressions. *Significant correlation (Pearson, $p < 0.05$). N = 17

p < 0.001, N = 32). Moreover, time of fatigue was significantly lower in the 140% compared to the 120% U_{crit} peak group (Mann-Whitney rank sum test, $T = 347$, $p < 0.001$). Generally, fish swimming at relative peak speeds below 2.5 body lengths s^{-1} did not become fatigued, while fish swimming above 2.8 body lengths s^{-1} all became fatigued within the 4 h test period (Fig. 3A).

When testing different periodicities with the same peak speeds of 120% U_{crit}, fatigue times were not statistically different (1-way ANOVA, df = 44, p = 0.771), being 113 ± 11, 119 ± 10, and 123 ± 10 min in the 0.5, 1, and 2 min period groups, respectively. Additionally, out of 18 fish tested per group, 3, 4, and 2 fish completed the 4 h test when using periods of 0.5, 1, and 2 min, respectively (Fig. 4A). Time of fatigue was neither correlated with relative swimming speeds within or across treatments of different periodicities at 120% U_{crit} peak currents (Pearson, p > 0.05, N = 45). Compared to using 1 min periods, the 1.5 h average fatigue time in the 120% groups was significantly higher than the 51 min of the 140% U_{crit} group (Mann-Whitney rank sum test, p < 0.001) (Fig. 4B).

4. DISCUSSION

We show that wave-like environments can be created in a small-scale laboratory setting and then be used for novel dynamic swim trials where the tolerance to such conditions in Atlantic salmon can be tested. This allows us to infer physiological limits to powerful waves at offshore aquaculture sites, and thereby provides valuable knowledge for evaluating potential new locations from a fish welfare perspective.

Overall, it was found that Atlantic salmon performed well in response to fluctuating water currents, adjusting their swimming efforts appropriately. The fish were able to endure intermittent peak currents that exceeded previously established threshold

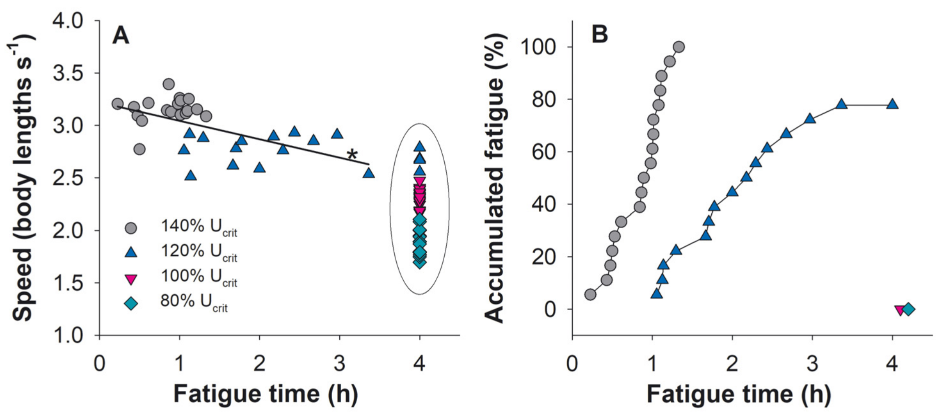

Fig. 3. Swimming endurance when exposed to fluctuating water currents with different peak speeds of a 1 min periodicity. (A) Individual relative peak swimming speed as a function of fatigue time in 4 treatment groups. Line with asterisk shows a significant correlation between swimming speed and time of fatigue in fish that became fatigued across treatment (Pearson, $p < 0.05$), and points encircled at the 4 h mark represent fish that completed the swim trial without becoming fatigued. (B) Accumulated percentages of fatigued fish over time. N = 18 per treatment. U_{crit}: critical swimming speed

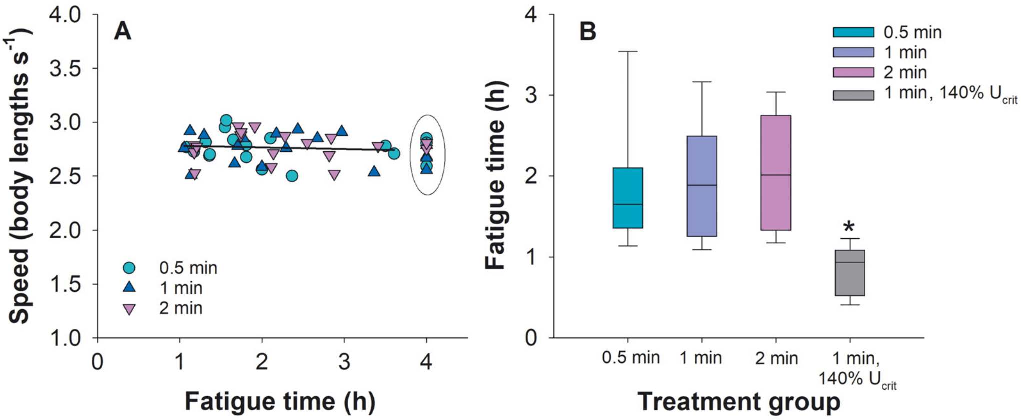

Fig. 4. Swimming endurance when exposed to fluctuating water currents with different periodicity with peak speeds of 120% U_{crit}. (A) Individual relative peak swimming speed as a function of fatigue time in 3 treatment groups. Line shows the non-significant correlation across treatments for those fish that became fatigued versus their relative swimming speed (Pearson, $p > 0.05$), and points encircled at the 4 h mark represent fish that completed the swim trial without becoming fatigued. (B) Boxplots of fatigue time in treatment groups where fish became fatigued (the 140% U_{crit} peak group and the three 120% U_{crit} peak groups). *Significant difference vs. the 1 min 120% U_{crit} group (Mann-Whitney rank sum test, $p < 0.001$). N = 18 per treatment. U_{crit}: critical swimming speed

values for sustained and critical (U_{crit}) swimming speeds without becoming fatigued. This suggests that constantly accelerating and decelerating swimming speeds did not require substantial anaerobic efforts relative to constant swimming at similar peak speeds, as initially hypothesized. As such, threshold values for fluctuating peak currents appear to be at least ~20% higher when compared to chronic current conditions. Testing different wave periods at the same peak current speed did not affect tolerance limits, suggesting that the peak current speed is more decisive than wave period when seeking to define novel welfare guidelines for wave-exposed offshore aquaculture sites. However, shorter wave periods than investigated here could potentially be more strenuous, as they would necessitate more frequent swimming accelerations and less intermittent downtime for momentary recovery.

4.1. Swimming capacity of Atlantic salmon in fluctuating currents

The U_{crit} measured in the present study was similar to previous work on Atlantic salmon of comparable sizes and similar acclimation temperatures when measured in the same swim tunnel system (Remen et al. 2016, Hvas et al. 2017a, 2021b). This suggests that the peak limits used when prescribing fluctuating current regimes can be considered representative for the general swimming capacity of cultured Atlantic salmon post-smolts. However, one must still consider that U_{crit} will vary depending on context. For instance, U_{crit} is sensitive to water temperature, dissolved oxygen saturation, and the size of the fish (Remen et al. 2016, Hvas et al. 2017a, Oldham et al. 2019). Moreover, compromised health owing to prevalent parasite infections in the farm environment can negatively affect swimming capacities of Atlantic salmon (Bui et al. 2016, Hvas et al. 2017b). When evaluating the welfare impact of various water currents and wave exposures at farm sites, key environmental and biological factors must therefore be carefully considered.

In the present study, we based the fluctuating peak currents on a percentage of a representative cohort-specific U_{crit} as a way to standardize test regimes around a constant water current that will cause physiological exhaustion regardless of context. This standardization should allow for a more generalized application of the reported threshold values for fluctuating peak currents when devising fish welfare guidelines for offshore aquaculture. Similarly, the limits of aerobic sustained swimming as well as optimal swimming speed for minimum cost of transport have also been standardized to percentages of the U_{crit}, being approximately 80–85% and 55–65% of the U_{crit}, respectively, across various sizes and acclimation temperatures in cultured Atlantic salmon (Beddow & McKinley 1999, Hvas et al. 2017a, 2021b, Hvas 2022).

All fish tested with fluctuating peak currents of 80 and 100% of the U_{crit} were able to endure the entire 4 h test period. This was a surprising result, as it was hypothesized that the periodic sudden swimming acceleration would require some recruitment of fast white anerobic muscles and then cause an accumulation of lactate that eventually would result in physiological exhaustion (e.g. Wood 1991, Kieffer 2000). The cost of swimming in flows with substantial velocity fluctuations was found to be higher than in steady flow conditions in shiner surfperch *Cymatogaster aggregata* (Roche et al. 2014). In a steady water current, Atlantic salmon are able to sustain swimming strictly aerobically via slow red muscles at speeds up to 80–85% of the U_{crit} (Beddow & McKinley 1999, Hvas & Oppedal 2017). Above this threshold, swimming efforts will be powered by a combination of red and white fibers and are therefore highly time-limited (Hudson 1973, Bone et al. 1978, Wilson & Egginton 1994). As such, in the 100% U_{crit} peak group, fish would have been swimming partly anaerobically during the peak period, yet they did not become fatigued during the 4 h test period. This suggests that the intervals with slower currents were adequate for sufficient recovery within the tested time frames. Yet, at 120% U_{crit} peak currents, most of the fish eventually reached fatigue regardless of wave periods, which effectively then defines a threshold limit for wave-imposed intermittent peak currents. Moreover, at 140% U_{crit} peak currents, all fish predictably fatigued sooner in a dose-dependent manner owing to a more rapid accumulating anaerobic burden. Finally, the average current speed experienced by the fish in the 140% U_{crit} peak group was approximately 80% of the U_{crit} and thus within the limit of sustained aerobic swimming for constant current speeds. Hence, when expressed as average current speeds over time, it is substantially more strenuous to endure fluctuations when compared to steady flows, as previously concluded by Roche et al. (2014).

4.2. Method considerations and applicability to aquaculture welfare guidelines

For the purpose of this study, a modified control system was installed so that cyclical peak currents could be generated automatically. Prior to testing fish, it was therefore necessary to investigate limitations in the system's ability to create fluctuating water current profiles that could be generated with regard to peak speeds and interval lengths. Those limitations would depend on how fast the motor could accelerate and decelerate water currents in the swim tunnel. Preliminary pilot tests without fish concluded that the shortest wave period that could be consistently maintained with peak speeds in the U_{crit} range of Atlantic salmon was approximately 30 s, with 15 s to reach the peak and 15 s to reach the minimum.

This meant that the wave periods used for the trials presumably were longer than what typically may be expected under natural circumstances (Wright et al. 1999, Albretsen et al. 2019). For instance, at exposed farms in the Faroe Islands, the longest reported wave periods ranged from 14 to 20 s, and additionally were described as more complex because of their varying durations (Dam 2015, Johannesen et al. 2020). However, these farm sites were shallow and close to the coast, and more extended wave periods are found in deeper and more open waters, where there is less influence from the seabed and the coast (Albretsen et al. 2019). Hence, depending on the specific locations of offshore farms, wave periods more similar to those tested in the present study may still occur. When performing environmental surveys of candidate aquaculture sites, detailed wave profiles over extended time scales will be necessary to evaluate actual exposure levels and fish welfare impacts, as previously has been done for water currents in ocean surveys (e.g. Jónsdóttir et al. 2019). Specifically, on the Norwegian coast, the 3 proposed offshore areas Norskerenna South, Frøyabanken North, and Trænabanken (Regjeringen 2022) should be described and evaluated in more detail than the median average and maximum of significant wave heights given in the presently available reports.

If we were to test shorter intervals with fluctuating water currents in future experiments, an even more powerful motor would be needed to provide faster accelerations, or a different type of setup would have to be designed. Such setups could also seek to provide different types of wave patterns, for instance by allowing flows to go back and forth, as in the setup used by Marcoux & Korsmeyer (2019). Generally, it would be easier to generate shorter wave periods in smaller setups than in the present swim tunnel design of ~2000 l. However, smaller fish sizes would then likely need to be tested, which could make experiments less relevant for applied aquaculture. In the present study, fish sizes of ~800 g were tested, which still is a relevant size for growing Atlantic salmon post-smolts in sea cages, but nevertheless represent the lower size ranges in a full production cycle, as harvest size typically is 5–7 kg. These considerations highlight some of the unavoidable logistical compromises in laboratory experiments when attempting to replicate complex real-life conditions. Realistically it may therefore not be feasible to construct a setup that can provide shorter wave intervals while also allowing for testing relevant fish sizes. For context of this scaling challenge, the more realistic wave-respirometer described in Marcoux & Korsmeyer (2019) tested fish of 5–10 g and 6–8 cm. Hence, field observations of Atlantic salmon coping ability will instead be required once it becomes possible at future offshore aquaculture sites.

We have limited knowledge on how Atlantic salmon behave within offshore cages in wavy conditions. The actual movement of a particle (similar to a neutrally buoyant fish without moving) in a wave is circular and involves continuous turns in direction, both horizontally and vertically. The fish will also experience variable gravitational forces depending on the position within and movement of the wave. The fish will respond, to an unknown degree, by movement towards the influence, similarly to being in the swim tunnel, where they coped adequately with the speed fluctuations. Even so, within medium to large regular sinusoidal waves with H_s (significant wave height) of 5 and 15 m, the particle movement in the upper 10 m of the surface layer ranges between 1–1.5 and 3–4 m s^{-1}, respectively (Tord Ludvigsen pers. comm.). Such speeds will clearly be above the thresholds found in this trial, but as fish may partly or fully follow the water movement, coping may occur if collisions with subspecies or net walls do not take place. Another coping behavior would be deeper swimming, as the circular water movement is also strongly reduced with depth (e.g. Kundu et al. 2016). In comparison to the Faroe Island studies using shallow cages of <20 and <30 m bottom depth (Dam 2015, Johannesen et al. 2020, 2022), future offshore cages will hopefully have substantial volume available at depth allowing salmon to swim deeper for shorter or longer periods and allowing them to stay within their physiological limits. Similar avoidance of detrimental farm environments has been repeatedly visualized as crowding responses away from extreme temperatures or low oxygen conditions within the water column (Oppedal et al. 2011, Dempster et al. 2016, Stehfest et al. 2017).

Welfare guidelines for Atlantic salmon at offshore aquaculture sites have until now mostly considered constant water currents and how they compare to the swimming capacities on various time scales (Hvas et al. 2021a). Here, U_{crit} and sustained aerobic limits of the fish represent acute thresholds in a worst-case scenario. Additionally, lower moderate current speeds lasting days or weeks are also important to consider, as they can impair growth performance and restrict voluntary behaviors (Farrell et al. 1991, Solstorm et al. 2015, McKenzie et al. 2021). Similarly, the present study only provides a quantification of acute limits to wave-like environments with powerful fluctuating water currents. Future efforts should therefore also assess long-term impact of waves on cultured Atlantic salmon with regards to fish welfare and growth performance. Perhaps it is possible to create moderate and persisting wave-like turbulence in laboratory holding tanks and then, for instance, monitor appetite and behavior over longer time periods. Regardless, we will eventually need to observe how the fish are performing at proper offshore farm sites, once these are up and running. Until then, laboratory trials such as the present study provide a robust fundament for understanding physiological limits of fish in novel environments, which will aid in choosing appropriate offshore farm sites from a fish welfare perspective.

Data availability. Raw data are readily available upon request to the corresponding author.

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