Assessing swimming capacity and schooling behaviour in farmed Atlantic salmon *Salmo salar* with experimental push-cages

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Abstract

The Atlantic salmon aquaculture industry is expanding to more exposed locations that often are characterized by occasional very strong currents. This necessitates new guidelines concerning acceptable animal welfare and a need for fundamental ethological knowledge in these high energy environments. To assess the critical current velocity in growing Atlantic salmon during commercially relevant conditions, a push-cage setup was constructed, which allowed for the exposure of an entire stocked sea cage to controlled current velocities generated by a fixated ship. Three replicates of a critical swim speed trial were made each containing approximately 1500 novel adult Atlantic salmon (3.4 kg). At 125 cm s^{-1} (1.97 BL s^{-1}) fish would start to become fatigued meaning that short durations of currents at or above this magnitude in an exposed setting would be detrimental to animal welfare. Furthermore, the normal circular schooling pattern started to become disrupted at current velocities of 30-35 cm s^{-1}, and above 45-65 cm s^{-1} all fish would stand on current evenly spread out in the entire sea cage. This change from a voluntary cruising speed at low currents to a swimming speed solely dictated by the environment at intermediate to high currents could become a significant stress factor if chronically exposed. Regarding welfare guidelines in exposed aquaculture, it is therefore important to both consider the magnitude and duration of current velocities when moving to new locations. Technological solutions in current damping through sea cages could potentially mitigate these challenges.

1. Introduction

To accommodate the continuous growth of the Atlantic salmon (*Salmo salar*) aquaculture industry, an increasing number of farming sites are likely to be established at remote exposed locations (e.g. Bjelland et al., 2016). Compared with traditional sheltered coastal environments, exposed locations offers several advantages such as higher water quality caused by a more rapid transport and dilution of waste products, higher levels of oxygen, stable vertical temperature and salinity gradients, and less interference and conflicts with other coastal activities, which should increase fish welfare, production capacity and reduce negative effects on local ecosystems (Holmer, 2010). However, since exposed sites are associated with greater wave action, stronger water currents, and also sheer remoteness, new advances in technology and infrastructure are needed (Loverich and Gace, 1997; Fredheim and Langan, 2009; Bjelland et al., 2016). More importantly, very little is known about how farmed salmon will cope in exposed environments with occasional strong water currents with respect to growth, stress levels, behaviour and welfare (Branson, 2008).

At sheltered farming sites current velocities outside cages are typically less than 20 cm s^{-1} (Johansson et al., 2007), where the swimming speed of *S. salar* is independent of the current velocity and caged fish forms circular schooling structures cruising at varying speeds of 0.3-1.1 body lengths per second (BL s^{-1}) (Sutterlin et al., 1979; Juell, 1995; Demster et al., 2009; Stien et al., 2016). Recently, a glimpse of swimming behaviours was observed at an exposed salmon farm in the Faroe Island, where the swimming pattern changed from circular, to a mixture of circular and standing on current, and then to all standing on current at low, intermediate and fast water currents respectively (Johansson et al., 2014). Since strong currents disrupt the circular schooling behaviour and forces the fish to swim at speeds dictated by the environment within the sea cage, this could severely compromise animal welfare if the magnitude and duration of water currents exceeds the swimming capacities of the fish.

To define the water current thresholds that secure salmon welfare in exposed aquaculture, it has been proposed to use the critical swimming speed (U_{crit}) (Remen et al., 2016). U_{crit} is obtained in swim trials by an incremental increase in water velocity until the fish fatigues (Brett, 1964), and theoretically provides a good estimate of swimming capabilities in fish that experience strong currents (Plaut, 2001). Prolonged exposure at or above U_{crit} will result in physiological exhaustion, which is associated with loss of locomotion control, depletion of muscle glycogen reserves, accumulation of lactate, release of catecholamines and even death (Wood, 1991; Burnett et al., 2014).

U_{crit} is dependent on experimental setup and is likely to be underestimated in small swim chambers since the burst and glide swimming gait is hindered (Peake and Farrell, 2006; Tudorache et al., 2007), while swimming in schools may reduce the cost of transport and thus improve swimming performance (Fields, 1990; Herskin and Steffensen, 1998, Svendsen et al., 2003). Furthermore, U_{crit} is size dependent and most studies only examine relatively small fish (e.g Brett, 1964, 1965, McKenzie et al., 1998, Wilson et al., 2007). Adequate methodology to assess the actual swimming performance of growing salmons in sea cages is therefore lacking.

Recent attempts to provide relevant data for the salmon industry used a very large swim tunnel design to swim small groups of Atlantic salmon (Remen et al., 2016; Bui et al., 2016). In the present study we take it further by performing an U_{crit} swim protocol on sea cages, each containing approximately 1500 large Atlantic salmon. This is achieved by generating controlled water currents from the propeller of an adjacent fixated ship, allowing us to simulate exposure to strong water currents at commercial scale conditions.

The objective of this study was to define the critical current velocity for growing *S. salar* in sea cages in their ambient environment, while also assessing schooling behaviour and the voluntary swimming speed during increases and decreases of current speeds. Furthermore, we evaluate the push-cage method for its biological relevance, including the variations in water current velocity from outside and within the cage.

2. Materials and methods

2.1. Experimental animals

After smoltification *S. salar* were reared in three sea cages (12 × 12 meter and 12 meter deep) holding approximately 10 000 fish each, at the Institute of Marine Research farm facility in Smørdalen, Masfjorden, Norway (60° N, 5° E). Fish were fed continuously from 8.00 to 14.00 everyday with commercial food pellets (9 mm Optiline, Skretting, Norway). Experiments were performed on May 13, 14 and 15, 2014 on fish that had been transferred by voluntary swimming from one of the production cages into the experimental push-cage the previous evening. Approximately 1500 fish were allowed into the push-cage with average weights of 3.40 ± 0.04 kg, stocking density of 11.3 kg m^{-3}, fork lengths (L_f) of 63.5 ± 0.3 cm and a condition factor of 1.29 ± 0.1 (based on a subsample where N = 614). Water quality was monitored with a CTD (Model SD204, Saiv A/S, Norway). Water temperature ranged from 7 to7.5 ºC, oxygen levels remained near saturation and salinity was 17.1, 30.7 and 31.6

at 1, 5 and 10 metre depth respectively. All experiments were conducted in accordance to the Norwegian regulation on animal experimentation under permit number 6569.

2.2. Push-cage setup

The experimental setup consisted of a ship that was fixated to a rigid docking bay on the downstream side of the fish cage, which allowed for strong controlled current generation by pushing the cage system. The ship "*Salma*" that was used to push the setup and thereby generating the current was 14.9 meter long, 6.3 meter wide and had two Sabb Iveco 420 HK motors (Hemnes Mekaniske Verksted i Nordland, Norway) connected to water jet systems for propulsion. The push-cage consisted of a circular net (12 meter in diameter and 4 meter deep) held in place by a circular plastic (PE) cage (Preplast Industrier AS, Norway), positioned on a 12 × 12 meter rigid steel cage frame. Extra weighting was provided up front to minimize, but not completely remove net deformation. An acoustic doppler current profiler (ADCP) velocimeter (600 kHz Aquadopp Z-cell profiler, Nortek AS, Norway) was placed 12 meter in front of the sea cage and 12 meter behind the sea cage to monitor current speeds at depths between 1.4 and 10.4 meter in 1 meter depth intervals. Three pan/tilt cameras (Orbit 3500, Steinsvik, Norway) were placed in the sea cage to observe swimming behaviour of the fish. See Fig. 1. for a conceptual drawing of the push-cage setup.

2.3. Experimental protocol

The push-cage protocols commenced at 13.00 each day after feeding was supplied to have satiated fish during the test. Current speed was increased incrementally every 15-20 minutes by 10-20 cm s^{-1}. A slight inaccuracy in increment interval and magnitude was unavoidable due to technical challenges in operating such a large scale setup, and continuous fine adjustments in engine power had to be made to keep flow speeds upstream from the push-cage stable. Once 15-30 (~1-2%) fish were lying in the back of the sea cage net unable to continue swimming freely, the water current speed was decreased at a pace corresponding to the previous increment intervals. Fish were observed until a circular schooling structure had been re-established. No fish died during the push-cage trials.

2.4. Observations and measurements

Changes in school structure, categorized as either circular, on current, or a mixture of these, were observed via underwater cameras at each speed. The current speed that initiated ram ventilation was noted. At current speeds where fish were swimming in a circular pattern, the relative swimming speed of 15 random fish in the direction against and with the current was measured via the cameras as the time to move one body length (BL). The voluntary swimming speed ($U_{voluntary}$) of the fish when swimming against the current was then calculated as:

$$U_{voluntary}\ (cm\ s^{-1}) = U_{camera}\ (BL\ s^{-1}) \cdot BL\ (cm) + U_{water}\ (cm\ s^{-1})$$

, where average BL of 63.5 cm (see section 2.1. Experimental animals) was used. At higher current speeds when all fish were holding a position on the current, the swimming speed of the fish would be equal to the current speed of the water.

3. Results

3.1. Current velocities

The recorded current speeds behind, in the front and beneath the sea cage during each swim trial are shown in Fig. 2. The current velocity at the time when ~ 1-2% of the fish fatigued was 126, 125 and 124 cm s^{-1} in trial 1, 2 and 3 respectively. These values are the average measured speed from 1.4-3.4 meters depth upstream and downstream the sea cage, and may not indicate the actual speed experienced by the individual fish since the flow speed varied substantially: At 1.4 meters depth behind the cage the current speed was 0.7-0.9 m s^{-1}, while at greater depths both in the front and the back of the sea cages, currents were above 140 cm s^{-1} in all trials and as high as 154 cm s^{-1}.

These differences indicate a notable current damping through the stocked sea cage. This is also evident from Fig. 2 when comparing the left and right panels, where water currents behind and in the front at 3.4-10.4 meters depth beneath the sea cages are similar, while the current velocity generally was lower behind the sea cage at 1.4-3-4 meter compared to in the front. The variation in current speed was greater at the depth of the sea cages (Fig. 2.), which can be ascribed to the complex interaction of the current with the dynamic structure of a stocked sea cage. Also, it was observed that at higher currents the sea cage would become compressed which decreased the volume available for the fish.

3.2. Swimming behaviour

At the lowest current velocities the fish were swimming in a homogenous circular structure. As the speed increased, the circular structure gradually became more skewed and elliptical-shaped, while some fish would start to stand on the current at 30-35 cm s^{-1}. Above

45-60 cm s^{-1} the circular structure was completely abolished and all fish were standing on the current. See Table 1 for a summary of the schooling structures at different current velocities. At the end of the swim trials when the current velocity had returned to its initial value, a circular schooling pattern had been re-established in all three sea cages.

The calculated voluntary swimming speed against the current in m s^{-1} is included on the left panels of Fig. 2, and indicates that while a circular structure is maintained, voluntary swimming speed is largely independent of the current velocity, where fish on average were swimming 48 cm s^{-1} corresponding to 0.76 BL s^{-1}. The relative swimming speed (BL s^{-1}) against and with the current while a circular structure is still maintained is shown in Fig. 3. Here it can be seen that initially, the swimming speed is similar at both directions of the circle, but as the current speed increases the movement of the fish slows down against the current, while it speeds up when swimming with the current, and thereby skews the circular structure.

During circular schooling the fish would only occupy a limited area. At high velocities when all fish were standing on current they were evenly spread out in the entire sea cage.

The onset of ram ventilation was first observed in the fish swimming at the front at ~65 cm s^{-1}, and was the dominating mode of ventilation for all fish swimming above 100 cm s^{-1}.

4. Discussion

4.1. The critical current velocity in sea cages

The first onset of fatigue in individual fish was initiated when the average current velocity upstream and downstream the sea cage at depths of 1.4-3.4 meter was 125 cm s^{-1} (1.97 BL s^{-1}). This value therefore marks the critical ambient current velocity for caged Atlantic salmon if the entire stock is to be protected. The actual current speeds experienced by fatigued fish could in theory be less since the blockage effect of nets causes a flow speed reduction inside net cages (Lee et al., 2008; Gansel et al., 2012; Zhao et al., 2015), together with a likely shielding effect of fish further upstream. A notable current reduction downstream of the sea cage was indeed measured, especially towards the surface. We did not measure the flow speed inside the cage, as that would require an elaborate setup to account for special flow variations, but the average of the upstream and downstream flow speed we report here should serve as a good estimate of the actual current conditions experienced by the fish.

Due to ethical concerns the current velocity was slowed down when ~1-2% of the fish fatigued meaning that the average value and variation in current tolerance of the entire stock was not obtained. The true mean U_{crit} for salmon in sea cages is therefore likely to be higher than 125 cm s^{-1}, since this value only corresponded to the lowest 1-2% of the experimental group.

Although U_{crit} in salmonids has been reported in countless swim tunnel studies, few exist on large adult fish. Here we briefly mention three examples: In reared *S. salar* the U_{crit} in adults (1.75 kg, L_f = 51.3 cm, 14°C) was 100 cm s^{-1} (Remen et al., 2016). In mature sockeye salmon (*Oncorhynchus nerka*) (2.41 kg, L_f = 61.4 cm, 19–21°C) the U_{crit} was 97 cm s^{-1} (Jain et al., 1998), however, this particular study was performed on cannulated animals in a relatively small swim chamber of 1.5 BL which could lead to an underestimated U_{crit} according to Peake and Farrell (2006). In wild caught adult *S. salar* (L_f = 55-60 cm, body weight was not reported) U_{crit} was an impressive 216 cm s^{-1} and 1.76 m s^{-1} at 18°C and 13°C respectively (Booth et al., 1997). These studies demonstrate a discrepancy in the swimming performance of adult salmonids, which likely is caused by differences in experimental setup, physical condition of the fish and various environmental factors (e.g salinity and temperature).

The fish used here were larger than in these previous studies (3.4 kg, L_f = 63.5 cm), and swimming capabilities increases with size (Brett, 1965). However, at 7-7.5°C the temperature was much lower compared to Remen et al. (2016), Jain et al. (1998) and Booth et al (1997). At such relatively cold temperatures swimming performance in salmonids is expected to be lower (Brett, 1964; Farrell, 2002). Also, our trials were purposely performed on fed fish to better approximate the conditions of growing salmon in sea cages, while it is common practice in traditional swim tunnel experiments to starve fish for at least 24 hours prior to experimental trials to avoid the confounding metabolic effects of specific dynamic action. Being fed to satiation led to a 15% reduction in U_{crit} compared to being fasted in rainbow trout (*Oncorhynchus mykiss*), since the maximum O_2 consumption is limited by the ability to take up and transport oxygen rather than the capacity to consume it at the tissues (Alsop and Wood, 1997).

Considering that swimming performance in our study likely was compromised by both temperature and feeding, and our estimate of a U_{crit} of 1.25 m s^{-1} only corresponded to the lowest ~1-2%, it is surprising that this value is substantially higher compared to both Remen et al. (2016) and Jain et al. (1998). Data from Booth et al. (1997) seems the most compatible with our findings in adult *S. salar* when taking environmental differences into account despite their study being performed on wild fish.

Having approximately 1500 fish swimming in a school in our trials might have improved performance by lowering the cost of transport in trailing positions. In pacific mackerels (*Scomber japonicus*) tail beat frequency was lower in schooling fish (Fields, 1990). Also, in European sea bass (*Dicentrarchus labrax*), tail beat frequency was 9-14% lower in fish swimming at the rear of the group, which was estimated to cause a 9-23% reduction in oxygen uptake (Herskin and Steffensen, 1998). However, in shortnose sturgeon (*Acipenser brevirostrom*) there was no difference in U_{crit} between testing fish individually and in groups (Deslauriers and Kieffer, 2011). The ability to take advantage of school swimming therefore seems to be species specific, and at this time it is unclear whether adult *S. salar* are able to reduce their cost of transport by swimming in schools.

It is difficult to directly compare the critical current velocity obtained here from a large scale push-cage experiment with U_{crit} data obtained in traditional swim tunnel studies, because these represents two different approaches in the assessment of swimming capabilities. Since our experimental setup to a much greater extent attempts to approximate a commercial farm setting exposed to strong currents, these data should be useful for the salmon industry when defining acceptable current limits in exposed aquaculture.

4.2. Swimming behaviour as welfare indicators

The gradual change in schooling structure from circular swimming to keeping a position on the current was recently observed at an exposed salmon farm, where the change from circular to a mixture of circular and standing on current was initiated at 35 cm s^{-1}, and above 47 cm s^{-1} all fish would stand on the current (Johansson et al., 2014). These threshold velocities for a change in schooling structure are similar to the findings in the present study (table 1). This indicates that the push-cage setup can be used as a tool to obtain representative data for a larger commercial scale setting. The fish used here had never previously experienced strong currents, yet their behavioural response was the same as in fish reared in an exposed environment with frequent current challenges (Johansson et al., 2014). This suggests an inherent preference in voluntary cruising speed independent of acclimation history.

At lower current velocities and circular swimming the voluntary cruising speed was 48 cm s^{-1} (0.76 BL s^{-1}), which is close to the observed threshold value for the complete disrupt of schooling behaviour where all fish stood on current. This indicates that *S. salar* will not maintain circular swimming when it is required to swim above its preferred swimming speed.

The movement of the circular structure was slowed down in the side against the current (Fig. 3), which further supports this, since the fish did not attempt to work harder as the currents increased while they were still swimming in circles.

Wild migrating salmonids have been found to consistently swim at average speeds close to ~1 BL s^{-1} (Drenner et al., 2012). This moderate swimming speed during migration has been suggested to be associated with an optimum cruising speed (Weihs, 1973), and in swim respirometry studies ~1 BL s^{-1} indeed corresponded to the minimum gross cost of transport (Brett, 1995). Considering the migratory behaviour of *S. salar* from a welfare perspective in aquaculture, it seems intuitive that on the long term current velocities inside sea cages should not exceed the voluntary swimming speed of the school structure, since that compromises the ability for the fish to express its natural behaviour.

In terms of production efficiency, it is well documented that moderate exercise provide several positive effects such as increased growth rates, higher protein content, improved aerobic capacity and better disease resistance in *S. salar* (Totland et al., 1987; Jørgensen and Jobling, 1993; Castro et al., 2011), which could be an important advantage in exposed aquaculture. However, chronic exposure at higher current velocities of 1.5 BL s^{-1} caused a substantial reduction in growth in *S. salar* post smolts (Solstorm et al., 2015). The current threshold for growth impairment is therefore higher than the preferred swimming speed, but lower than the critical current velocity (~2 BL s^{-1} for adults).

Above 65 cm s^{-1} an increasing number of fish started to ram ventilate. In *O. mykiss* ram ventilation caused a 10.2% decrease in oxygen uptake when swimming at constant speeds by avoiding the metabolic cost of active gill ventilation (Steffensen, 1985). Ram ventilation thus marks an adaptation to more effective sustained swimming when the oxygen requirements are higher. The onset of ram ventilation in *S. salar* was at higher flow speeds than the speed at which complete disrupting of circular voluntary swimming occurred. Since ram ventilation is an easily observable trait, it can be used to assess welfare status, where it would indicate that the fish are aerobically challenged. Prolonged swimming with ram ventilation would increase the risk of physiological fatigue and certainly impair growth.

Swimming in a circular structure might reduce stress and improve growth efficiency due to less confrontations within the sea cage (Juell, 1995), while increased appetite has been observed to coincide with a change from unstructured to circular schooling (Fernö et al., 1988). Concerning acceptable fish welfare and optimal growth rates, it may be argued that new exposed location for salmon farming should provide an environment where the fish are allowed to form circular schooling structures for the majority of the time or being able to swim at speeds ranging within their preferred intervals. Further studies need to reveal more specifically what is voluntary/preferred swim speeds within sea cages, and how it varies with time of day, season, depth and other environmental fluctuations or management specific strategies.

4.3 Technological and practical implications for exposed aquaculture

As current velocity increased, the sea cage would become more and more deformed which reduced the volume available for the fish. A current velocity of 35 cm s^{-1} has previously been found to cause a 40 % reduction in sea cage volume by lifting the bottom and deforming the side walls of the net at an exposed salmon farm on the Faroe Islands (Lader et al., 2008). The technology for making sea cages that are able to withstand strong water currents is well developed (Fredheim and Langang, 2009). However, they do not avoid volume changes meaning that new designs are needed for more robust sea cage structures. From a fish welfare perspective, such new designs should also seek to dynamically affect water exchange rates in dependence of upstream flow speed to help prevent exposure to unacceptably high currents within sea cages. Furthermore, currently the legal biomass limit for sea cage stocking density in Norway is 25 kg m^{-3}. If exposed sea cages are chronically deformed with a substantial reduction in available volume for the fish, this welfare standard might not be achieved in practice.

Vertical variability in temperature, salinity, light and dissolved oxygen exist within sea cages, where salmon are known to occupy a specific depth corresponding to active trade-offs between these gradients in their preferred environment (Oppedal et al., 2011; Stien et al., 2013, 2016). Interestingly, at high currents in the present study fish were observed to be evenly spread out and thereby presumably overruling other environmental variables. Strong current velocities could thereby override preferences in other important environmental factors. Thus, if strong vertical gradients in temperature and dissolved oxygen are present within the sea cage (e.g. Oppedal et al., 2011; Stien et al., 2013), then these should be considered in welfare assessments at exposed locations, since they may impair swimming capabilities (Brett, 1964; Jones, 1971).

Finally, stronger currents will have practical implications on feeding. Normally feed is distributed in the centre of the sea cage, but at locations with an appreciable amount of current action it would be logical to distribute feed at a location further downstream in the sea cage to increase the drift time of food pellets where the fish are able to eat them. During short periods of very high current velocities it might not even be feasible to feed the fish, if they are unable to catch food pellets while swimming. The exact placement of feeders would depend on the sinking rate of pellets, current velocities, net deformation and the distribution of fish in the cage. Furthermore, the metabolic cost of feeding may also reduce swimming performance (Alsop and Wood, 1997), meaning feeding protocols ideally should be monitored and adjusted to the changing weather conditions on site for optimal production.

5. Concluding remarks

The swimming behaviour and school structure of *S. salar* can be utilized as a simple yet effective assessment of the current condition in sea cages. When defining welfare parameters we suggest that long term exposure should not exceed the voluntary swimming speed (e.g having fish standing on current ram ventilating for prolonged periods), and short term peak currents should not exceed the critical current velocity reported here since physiological fatigue, which causes a tremendous amount of stress and sometimes even death, is not acceptable in modern aquaculture practices.

Assessing swimming performance in large groups of adult *S. salar* with experimental push-cages provided a viable method in obtaining relevant data on a commercial scaled level. To further expand on the development of suitable welfare guidelines in exposed aquaculture it will be highly relevant in future push-cage studies to also investigate how factors such as fish size, feeding, acclimation history, genetics and seasonal changes in temperature affects swimming capabilities, while a thorough documentation of both frequency and magnitude of strong currents at exposed locations are needed.

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Author contributions

Experiments were designed and conducted by O.F., D.S., T.V., J.O.F., L.C.G. and F.O. M.H. analysed data and prepared figures. The manuscript was written by M.H. with all co-authors providing valuable input and approving the final version.

Competing financial interests

The authors declare no competing financial interests.

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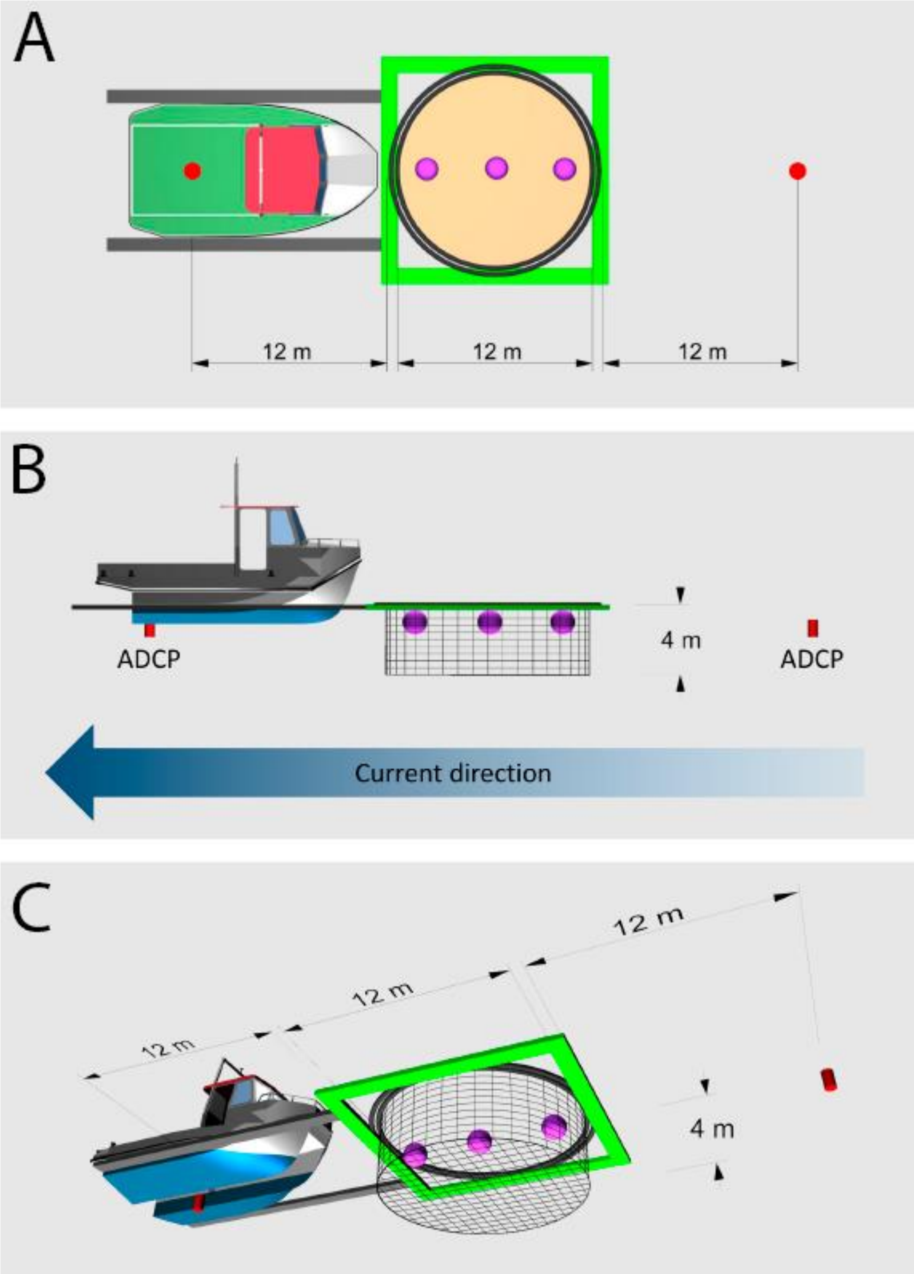

Fig. 1. Conceptual drawing of the push-cage setup as seen from above (A), from the side (B) and from bellow (C). Acoustic doppler current profilers (ADCP) are indicated by the red cylinders, while purple circles are the position of the pan/tilt cameras.

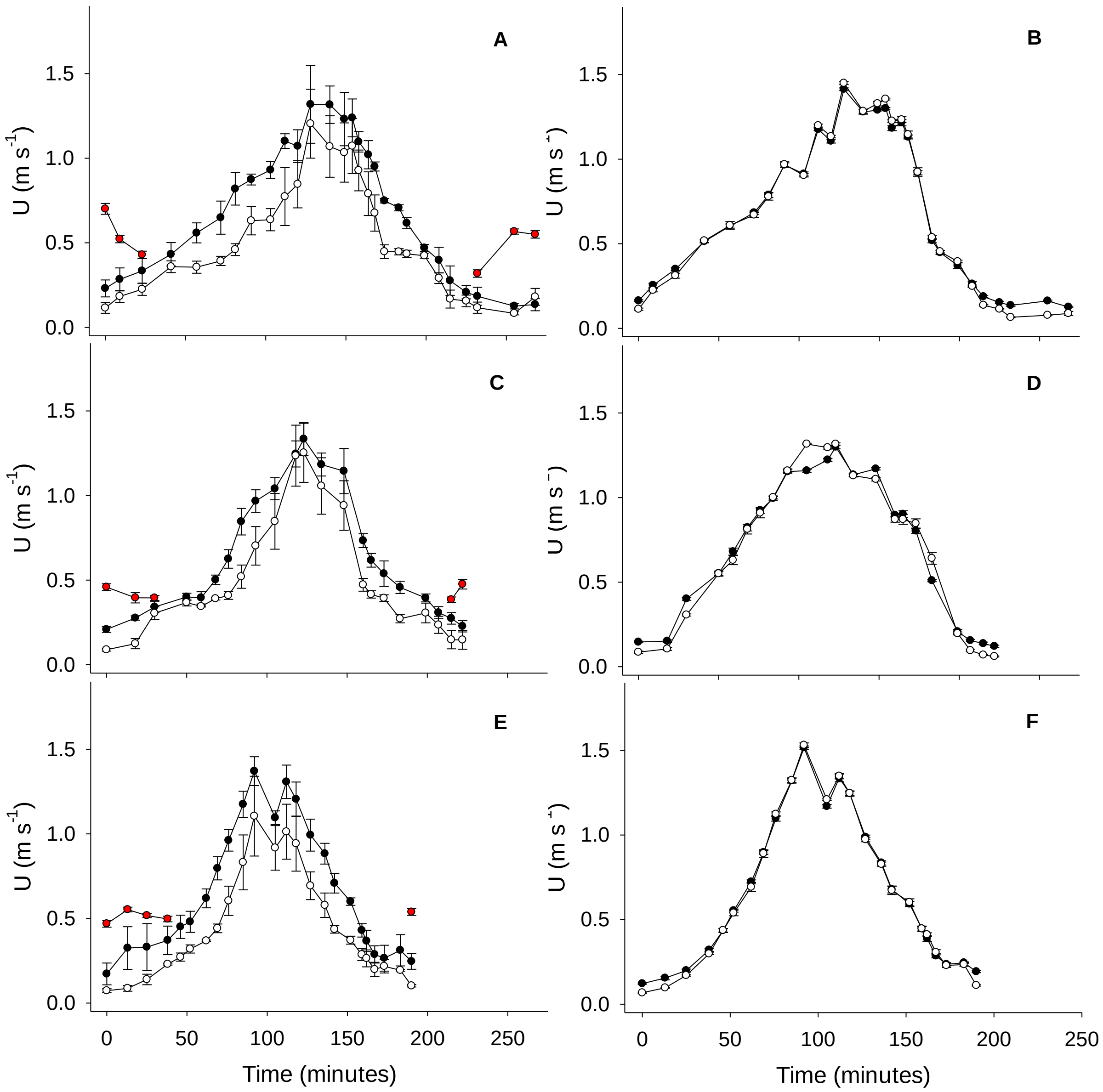

Fig. 2. The current profiles in front of (filled circles) and behind (open circles) the push cages during swim trials, where panels to the left are current profiles at the depths of the sea cage (1.4-3.4 meter), while panels to the right are beneath the sea cage (4.4-10.4 meter). A and B are trial 1, C and D are trial 2, and E and F are trial 3. The voluntary swimming speeds are indicated on the left panels (red triangle). At higher velocities the swimming speed of the fish equals the current speed in the water. Data are mean ± S.E.M.

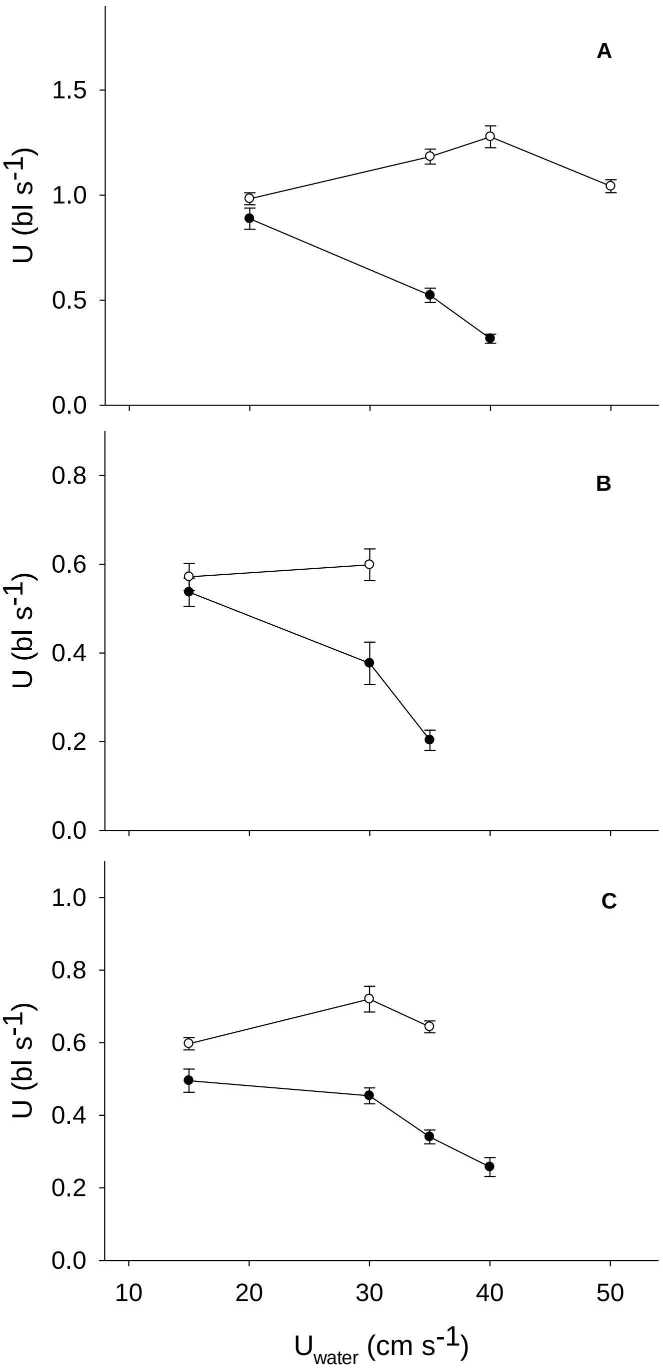

Fig 3. The relative swimming speeds (U) against (filled circles) and with (open circles) the current as the water current velocity increases while a circular schooling structure is still partially maintained. A, B and C are trial 1, 2 and 3 respectively. N = 15. Data are mean ± S.E.M.

Table 1. The patterns in schooling structure of caged Atlantic salmon (circular swimming, standing on current or a mixture of these) at different current velocities (cm s^{-1}) set during the three push-cage trials.

	Circular	Mixture	All on current
Trial 1	20	35-60	65+
Trial 2	15-30	35	45+
Trial 3	15	30-40	50+