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'Snorkel' sea lice barrier technology reduces sea lice loads on harvest-sized Atlantic salmon with minimal welfare impacts

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ABSTRACT

The infestation of farmed Atlantic salmon (*Salmo salar*) by ectoparasitic sea lice (*Lepeophtheirus salmonis*) presents a need for new approaches to parasite control. One option is the use of 'snorkel' sea lice barrier technology, which restricts salmon from accessing the surface except via a vertical chamber impermeable to sea lice larvae. This prevents the salmon from swimming at the depths where infective sea lice are most abundant. Before snorkels can be implemented in commercial sea-cages, knowledge is required about their effects on salmon welfare and growth. Here, we installed snorkels of 4 m depth into three $12 \times 12 \times 12$ m^3 cages, and recorded the lice infestation of stocked fish along with their growth, behaviour, and snout and fin condition over a 12-week period. Three standard sea-cages were utilised for comparison, and all six cages were stocked with ~3500 salmon (2.3 ± 0.6 kg). After 3, 6, 9, and 12 weeks, fish in snorkel cages had 65, 24, 43, and 56% lower lice levels than in standard cages, respectively. Salmon in both snorkel and standard cages grew similarly well and we detected little or no adverse effects on fish mortality or welfare. The results indicate that snorkel sea-cage barrier technology provides a promising new tool in parasite management in salmon aquaculture.

Statement of relevance

The ectoparasitic sea louse (*L. salmonis*) is the key obstacle for further expansion of industrial on-growing of salmon in sea-cages in Norway and Scotland. There is therefore high demand from both the industry and the governments for new environmental friendly technologies that reduce the sea louse problem. Here we demonstrate that snorkel sea cages can be used to control lice loads under the problematic autumn months for high valued slaughter ready salmon without significant adverse effects on fish welfare and fish growth. This study is therefore highly relevant for the Aquaculture journal.

1. Introduction

The ectoparasitic sea louse (*Lepeophtheirus salmonis*) is a key obstacle for continued industrial on-growing of salmon in sea-cages in Norway and Scotland (Jones and Beamish, 2011). To remain below allowed lice levels, salmon farmers often have to treat their salmon repeatedly with drugs administered through the food, chemical baths and through the use of cleaner fish (Torrissen et al., 2013). These treatments can constitute more than 10% of production costs (Iversen et al., 2015), and lice are developing resistance to the chemical therapeutants (Grøntvedt et al., 2014; Helgesen et al., 2015). Cleaner fish have proved effective against sea lice, but there is limited availability, questions about their welfare (Treasurer and Feledi, 2014), and concern they can be a vector for transmitting disease (Murray, 2014a). Therefore, the salmon industry is urgently attempting to develop an array of new methods to treat or reduce infestation by sea lice.

L. salmonis occurs naturally in the northern Atlantic ocean and has evolved to position itself in the upper part of the water column to increase encounter probability with potential hosts (Heuch et al., 1995; Hevrøy et al., 2003; Johannessen, 1977). Based on this aspect of sea lice behaviour, one possible solution is to prevent or limit the contact farmed salmon have with surface waters. Several new management techniques and technologies that use this principle are being tested and implemented: closed sea-cages where the water is pumped in from the deep (Strand et al., 2013), plankton sheeting enclosing each cage to filter the surface water (Næs et al., 2012), tarpaulin wrapping around the upper part of each cage to direct the surface water around

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cages (Frank et al., 2015; Stien et al., 2012), submerged lights and feeding to attract salmon to deeper depths (Frenzl et al., 2014), and snorkel sea-cages (Oppedal et al., under review; Dempster et al., under review) and submerged sea-cages (Korsøen et al., 2012) that hold salmon below the surface water. Before these technologies can be introduced industry-wide, their effects on lice infestation must be confirmed and their impacts on fish welfare evaluated.

Here, we focus on the use of snorkel sea-cages. These are sea-cages with a net roof that keep the salmon deep in the water column, while allowing them to access the surface via an enclosed tarpaulin tube (a snorkel). Snorkel sea-cages offer distinct advantages over fully submersible sea-cages, as they allow salmon access to the surface. Salmon are physostomes and must re-fill their open swim bladder by gulping air in the surface (Saunders, 1965) to maintain buoyancy when they return to swim at depth. In contrast, fully submersible cages prohibit salmon from accessing the surface, and lead to a range of negative effects on growth and behaviour which stem from negative buoyancy (Dempster et al., 2008, 2009; Korsøen et al., 2009).

The potential of snorkel sea-cage technology in reducing sea lice infestation was demonstrated by Oppedal et al. (n.d.), finding salmon post-smolts in sea-cages with 3 m deep snorkels had 77% less lice than those in normal sea-cages. This first study of the snorkel principle was performed on newly-transferred spring smolts over summer. The overall focus was on lice infestation, rather than fish behaviour and welfare. A second study was therefore conducted to examine behaviour and individual growth rates of salmon stocked in snorkel cages vs. salmon in standard cages (Dempster et al., n.d.). This study followed medium-sized salmon during winter and found minor negative effects on production performance and behaviour from the snorkel technology. The authors suggested that the observed minor effects on behaviour and reduced snout condition may be further ameliorated if the technology is scaled-up to full industrial size.

The potential for using snorkel sea-cages on large salmon during autumn with commercial stocking densities is of particular interest. The autumn months are the most problematic period for salmon farmers to control lice loads. During this period, large biomasses of high value farmed salmon are held prior to slaughter. High host availability at the farms, in combination with high water temperature leads to short generation times from larvae to egg-producing adults (Murray, 2014b), and simultaneous return of wild salmon and build-up of lice on coastal sea trout all contribute to increased abundance of sea lice larvae (Torrissen et al., 2013). This is therefore a critical stage of production, especially since oral medicine must be avoided near harvest and the potential costs associated with stressing or overdosing fish during topical treatments are high. We therefore aimed to test if the snorkel lice barrier technology is effective at preventing lice infestations without compromising fish welfare and growth in autumn for harvest-sized salmon.

2. Materials and methods

2.1. Location, experimental setup and design

The study was conducted in Autumn 2013 at the Institute of Marine Research aquaculture station in Austevoll, western Norway (~60°N). The sea-cage facility at the station has 12 × 12 m steel cages in two rows across the tidal current directions (East–West, and West–East). The experiment used three snorkel sea-cages and three control sea-cages evenly dispersed across the two rows. The snorkel sea-cages had a net roof at 4 m depth, with a tarpaulin-enclosed snorkel rising from the centre of the roof to the surface (Fig. 1). Both the snorkel and the control sea-cages had 12 m deep nets. On September 4, the sea-cages were each stocked with ~3500 fish with a mean weight of 2.3 ± 0.6 kg (mean ± SD). This gave an effective stocking density of 5 kg m^{-3} in the control sea-cages and 7 kg m^{-3} in the snorkel sea-cages. Throughout the experimental period, the fish were fed in excess via a hose distributing the feed at the surface in the cage centre, and in the case of the snorkel cages, at the surface within the snorkel. Daily environment profiles of the water column were collected at a reference point outside the sea-cages, using a conductivity, temperature and depth (CTD) sensor (SD204, SAIV AS, Bergen, Norway) from the surface to 12 m depth.

2.2. Lice infestation levels

Every third week (sample points 1–4), 20 fish were netted from each cage, killed by a blow to the head, and the infestation levels assessed on each fish. The number of attached lice were counted and classified according to life stage: chalimus 1, chalimus 2, pre-adult 1, pre-adult 2 (male and female) and adult (male and female with or without egg-strings). The chalimus development stages have traditionally been divided into four (chalimus I, II, II and IV), but recent research suggest that there is only one moulting (Hamre et al., 2013) and we therefore divided chalimus into only two categories. Due to very high lice loads in the control sea cages, the fish in all cages were topically deliced the day after the second sampling (AlphaMax®), and since this de-licing was not successful, also the day after the third sampling (Salmosan®). To ensure independent infestation rates from sample point to sample point, and data unaffected by the de-licing events, the statistical comparisons between groups were done using the numbers of newly attached lice (i.e. the non-adult stages).

2.3. Population swimming depth and total echo strength

The swimming depth distributions of fish populations in snorkel and control sea-cages were continuously recorded throughout the experimental period using a PC-based echo integration system (Lindem Data Acquisition, Oslo, Norway; described by Bjordal et al. (1993) and their use reviewed by Oppedal et al. (2011)). The transducers were positioned below the centre of each cage at ~15 m depth, facing upwards with a 42° acoustic beam. The total strength of the returned echo signal is indicative of the total swim bladder volume of the biomass that is present within the range of the acoustic beam (Ona, 1990). Therefore, the total echo-strength was monitored over the experimental period to assess whether swim bladder volumes were affected in snorkel cages, where there was the possibility that fish would avoid re-filling their swim bladder at the surface, compared to controls (Korsøen et al., 2009).

2.4. Growth, snout and fin condition

At the start (sample point 0), middle (sample point 2) and end of the trial (sample point 4), 100 fish from each of the six cages were captured and measured for weight in g, fork length in cm and snout and fin condition. Fulton's condition factor (Fulton, 1904) was calculated as $100 \times \text{weigh} \times \text{fork length}^{-3}$. Snout condition was scored 0 if no damage was evident, 1 for minor wear or damage, and 2 for severe wear or damage. The condition of dorsal and caudal fins was scored with an index from 0 (undamaged) to 5 (complete degradation) based on the method described in Hoyle et al. (2007). Fulton's condition factor was calculated as $C = 100(\text{weight} * \text{length} - 3)$.

2.5. Swimming speed and surface activity

To observe changes in swimming speed, we used cameras submerged to the depth of the school in each cage. Swimming speed measurements were undertaken at least once a week throughout the trial at ~10:00 AM, and once after the snorkels had been removed at the end of the trial. Swimming speeds were recorded as body lengths s^{-1} by measuring the time taken for the snout and then the caudal fin to

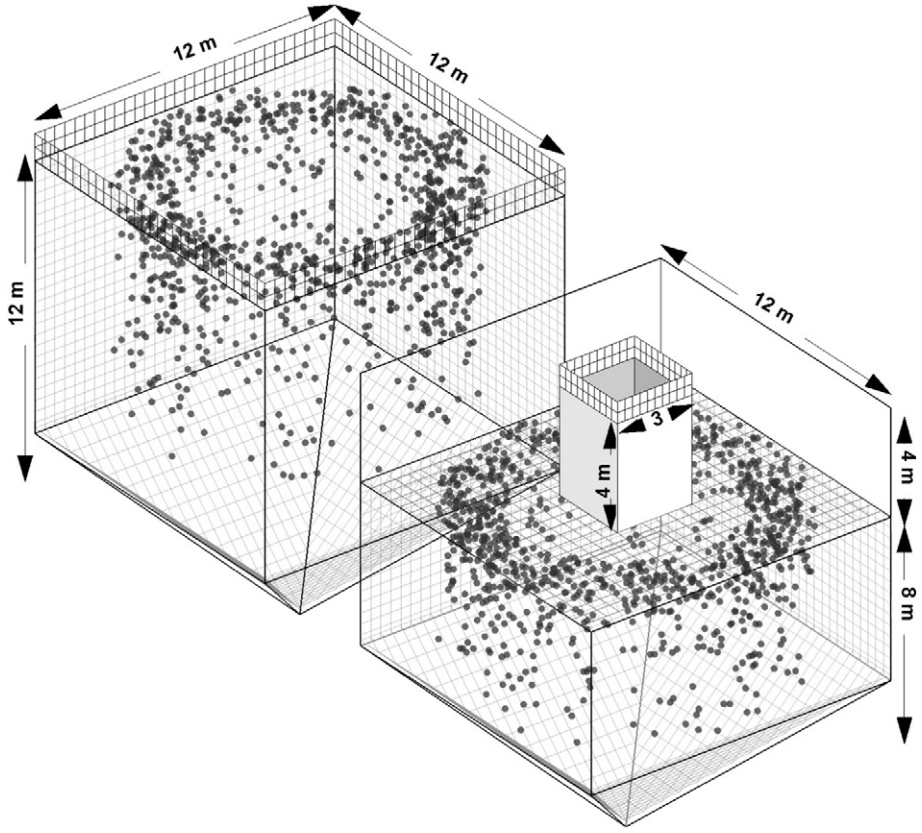

Fig. 1. Schematic illustration of a control cage (left) and a snorkel cage (right). The cages were 12 × 12 m^2 and 12 m deep. The snorkel roof was at 4 m depth and the 3 × 3 m^2 and 4 m deep snorkel was from the centre of the roof to the surface and 1 m above. Black dots within the cages represent salmon.

pass a vertical reference line within the cage (Dempster et al., 2008). Speeds were recorded for a total of 30 randomly chosen individuals: 15 individuals while the camera was facing west, and 15 when facing east. This was to take into account any differences in swimming speeds due to the two main current directions whereby fish swimming upstream and downstream will display different swimming speeds (Johansson et al., 2014).

On days that swimming speeds were measured, the number of jumps or rolls in a 5 min period was recorded in each cage. This gave an indication of swim bladder re-filling behaviour between snorkel and control cages. Further, surface activity was intensively monitored following snorkel removal. All counts were converted to jumps $fish^{-1}$ min^{-1}.

2.6. Statistical analyses

Data analysis was performed using R software Version 3.1.0 (Copyright 2009, The R Foundation for Statistical Computing, Vienna, Austria). For each sample point, deviance in lice count data per fish were modelled using generalized linear models with quasi-Poisson errors, as recommended for count data with over dispersion (Crawley, 2012), and with treatment (snorkel or control) and cage number (1–6) as explanatory factors (function glm, R). We conducted similar analyses for the snout and fin condition data, but since this data was proportional (proportion of fish with each damage) the error distribution was set to binomial (Crawley, 2012). For the weight and condition factor data, analysis of variance was performed with normally distributed errors (function aov, R). Consistency of variance and normality of errors were confirmed with model checking plots (function plot, R). Aggregated values below represent mean ± standard error.

3. Results

3.1. Environmental conditions

During the experimental period, the water temperature decreased from ~16 to ~9 °C (Fig. 2A). At the start, water near the surface was warmer than deeper water, but after a few days this switched to warmer at lower depths, with several periods of uniform temperature from the surface down to cage bottom (Fig. 2A). Salinity conditions varied from periods with a clear gradient from 33 ppt at lower depths to 20–24 ppt near the surface, to periods with a less clear gradient or 33 ppt in the entire water column (Fig. 2B). Times with little or no temperature gradient typically coincided with a lack of distinct salinity gradient (compare Fig. 2A and B).

3.2. Population swimming depth in the control cages

Fish in the control cages aggregated at different depths throughout the trial (Fig. 3A). In the two first weeks they predominantly occupied the upper 5 m, then descended to between 4 and 8 m, before ascending to between 1 and 6 m in the days before sample point 1. After sample point 1, these fish generally swam below 4 m during the day, while spreading out and utilised also the water above 4 m during the night. In snorkel cages, the fish were by design from 4 to 12 m, but there was still variability in swimming depths between day and night, with fish tending to stay slightly shallower and even move into the snorkel at night (Fig. 3B).

3.3. Lice infestation levels

At the observed temperatures (Fig. 2), salmon lice moult into adult stages within three weeks (Johnson and Albright, 1991). Thus, the non-

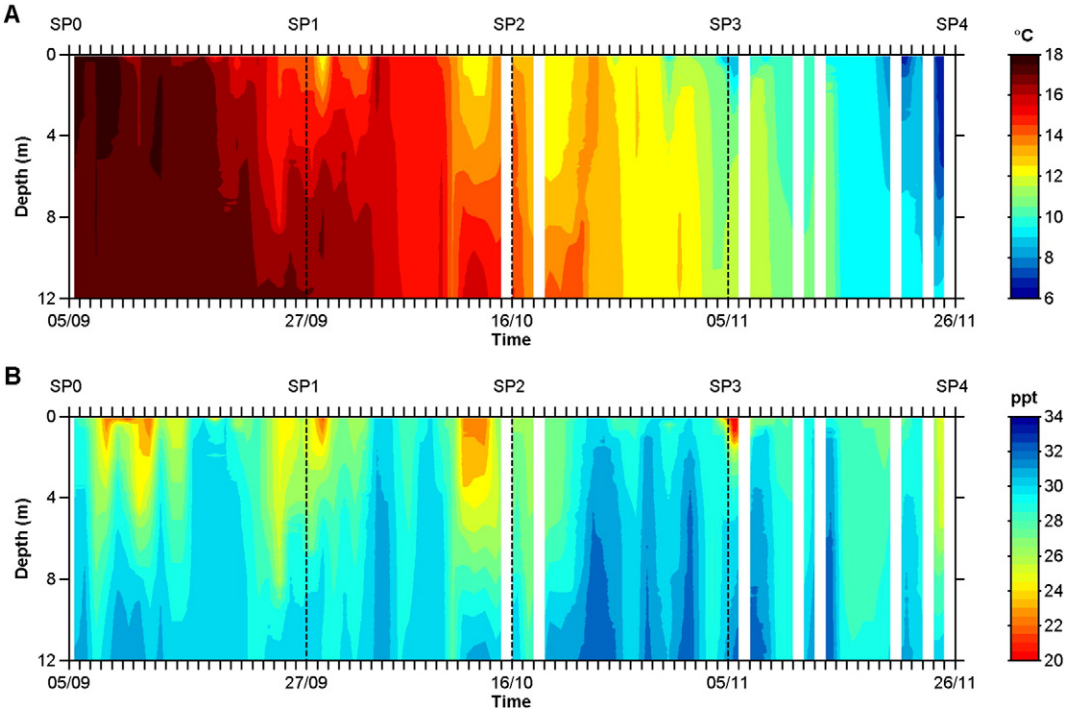

Fig. 2. Environmental conditions at the salmon farm location from 0 to 12 m during the experimental period. A) Temperature and B) salinity. The dates of sample points (SP) 0–4 are indicated by vertical hatched lines.

adult lice at each sample point can be considered new infestations. The counts of non-adult lice (new infestations) significantly decreased on snorkel fish compared to control fish by 65% ($p < 0.001$, $t = 8.8$) at sample point 1, 24% ($p = 0.001$, $t = -3.3$) at sample point 2, 43% ($p < 0.001$, $t = -6.0$) at sample point 3, and 56% at sample point 4 ($p < 0.001$, $t = -5.5$). The abundance of individual stages on snorkel fish was reduced by as much as 72% compared to control fish, though there were also periods where no decrease in an individual stage occurred (Fig. 4).

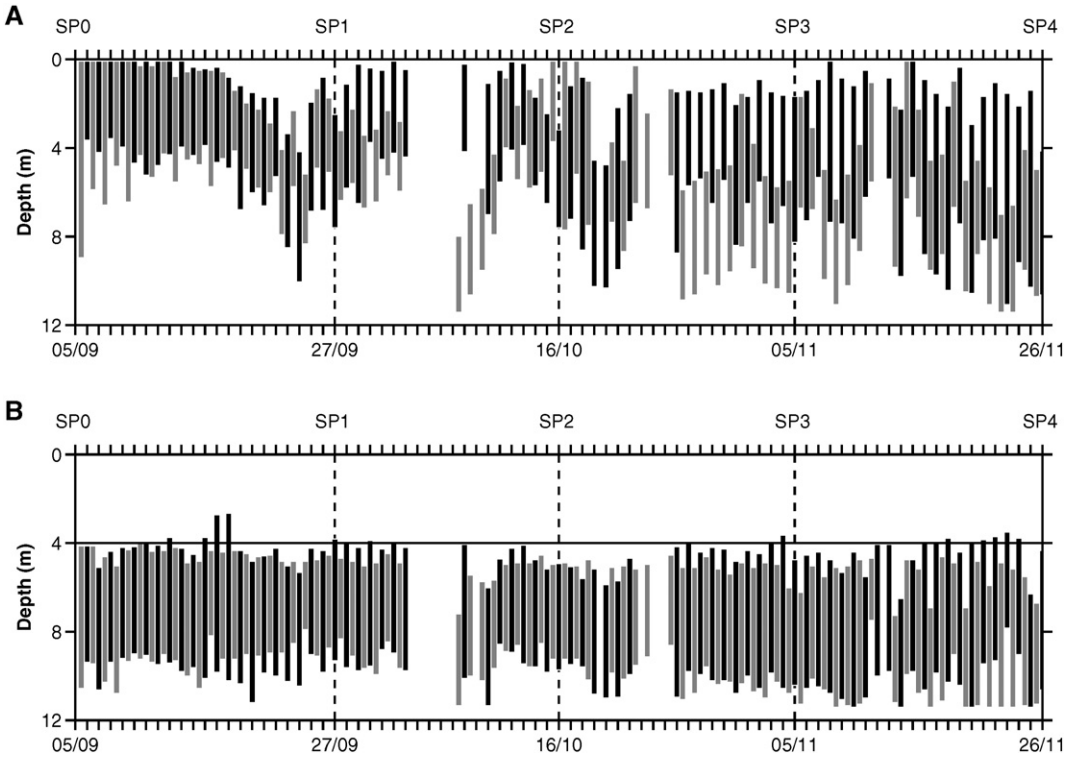

Fig. 3. School position during the day (grey bars) and at night (black bars). A) Control sea-cages, B) snorkel sea-cages. School position is defined as at least 75% of fish in each treatment group being positioned within the depths indicated by the bar. The dates of sample points (SP) 0–4 are indicated by vertical hatched lines, and the position of the roofs in the snorkel cages is indicated by a horizontal line at 4 m.

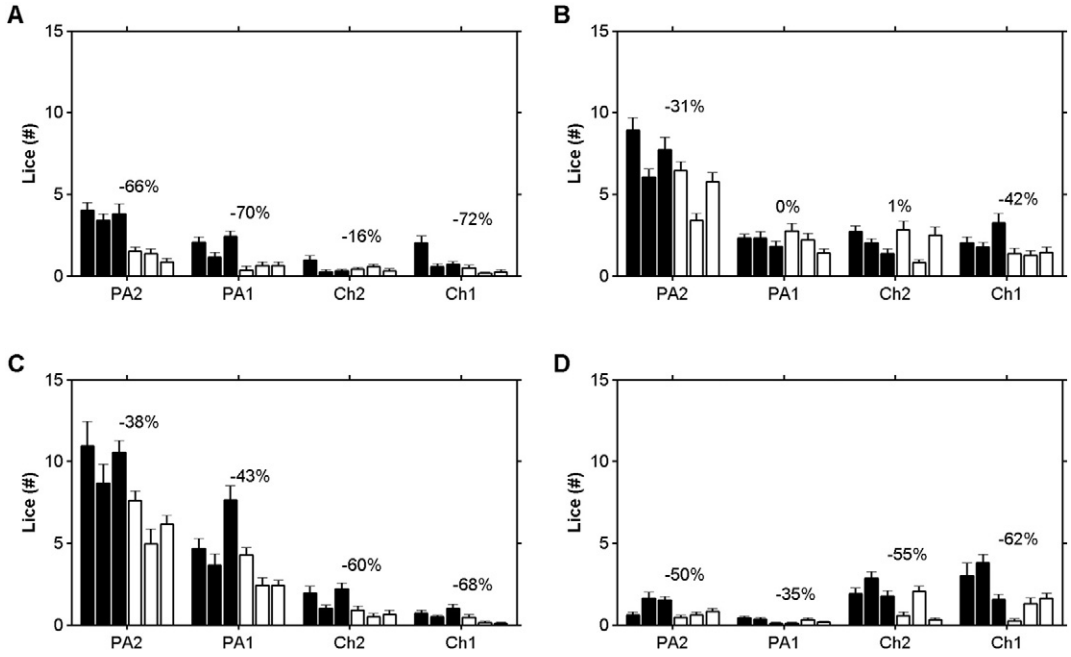

Fig. 4. Mean number (±SE) of pre-adult 2 (PA2), pre-adult 1 (PA1), chalimus 2 (Ch2) and chalimus 1 (Ch1) lice stages per cage for each sample point. Black and white bars indicate control and snorkel cages, respectively. Percentage differences between treatment groups are indicated above each stage. A) Sample point 1, B) sample point 2, C) sample point 3 and D) sample point 4.

3.4. Population total echo strength

Relative total echo strength overlapped between control and snorkel cages in the first six weeks of the experiment (Fig. 5). Then the relative echo strength for the fish in control sea-cages increased to 100–200%, while the relative strength for the snorkel cage fish remained between 50–100 % of initial echo strength until the snorkels and roofs were removed. In the days before and after the snorkels and roofs were removed, the echo strengths of the snorkel cage fish were 100% relative to original levels, with a peak slightly above 100% on the day they were removed (sample point 4, Fig. 5).

3.5. Swimming speed and surface activity

Mean swimming speeds were 0.5–1.1 BL s^{-1} for fish in the controls and 0.5–1.0 BL s^{-1} for those in snorkel sea-cages. There were no consistent differences in swimming speeds between treatment groups over the experimental period (Fig. 6A). During the experimental period, control cage fish generally had a greater jumping frequency than fish in the snorkel cages (4.2 ± 0.3 vs. 2.7 ± 0.3 jumps $fish^{-1}$ day^{-1}, $p < 0.001$, $F = 22.9$) (Fig. 6B), and when the roof had been removed (after sample point 4) there was an increase in surface activity for the fish in the former snorkel sea-cages (before 2.1 ± 0.2 compared to after 7.5 ± 0.8 jumps $fish^{-1}$ day^{-1}, $p = 0.018$, $t = -6.4$) (Fig. 6B).

3.6. Snout and fin condition

Prior to the first day of the experimental period (sample point 0), the percentage fish with severe snout damages (score > 1) were almost 0 for both the control and snorkel groups (Table 1) (0 vs. 1%, $p = 0.995$, $z = 0.006$). Mean percentage fish with severe snout damage increased to 5–6% at sample point 2 (Table 1), and also here there was no significant difference between the fish in the controls and the snorkel sea cages (5 vs. 6%, $p = 0.363$, $z = 0.7$.). But at sample point 4 the mean percentage fish with snout damage had increased to 31% in the snorkels, but had only increased to 21%, in the control sea-cages (21 vs. 31%, $p < 0.006$, $z = 2.8$).

Unfortunately, there was for some reason (see discussion) differences in fin damage already at sample point 0 (Table 1), with significantly more fin damage in the control sea-cages than in the snorkel sea-cages (dorsal fin: 93 vs. 84%, $p < 0.001$, $z = -3.5$) (caudal fin: 39

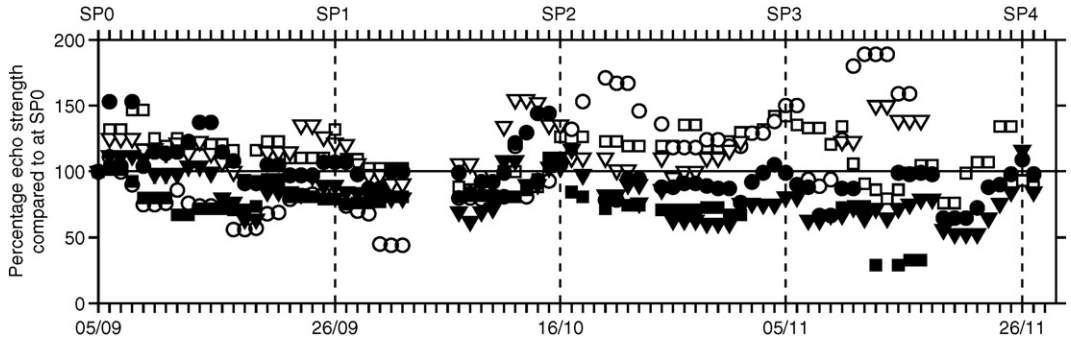

Fig. 5. Percentage of total echo strength relative to that at the start of the experiment (sample point 0) for each of the six cages. The control cages have white symbols and the snorkel cages have black symbols. The three cages in each group are indicated by square, circle or triangle symbols. The dates of sample points (SP) 0–4 are represented by vertical hatched lines and the horizontal line is the percentage echo strength from the first day of trial, i.e. 100%.

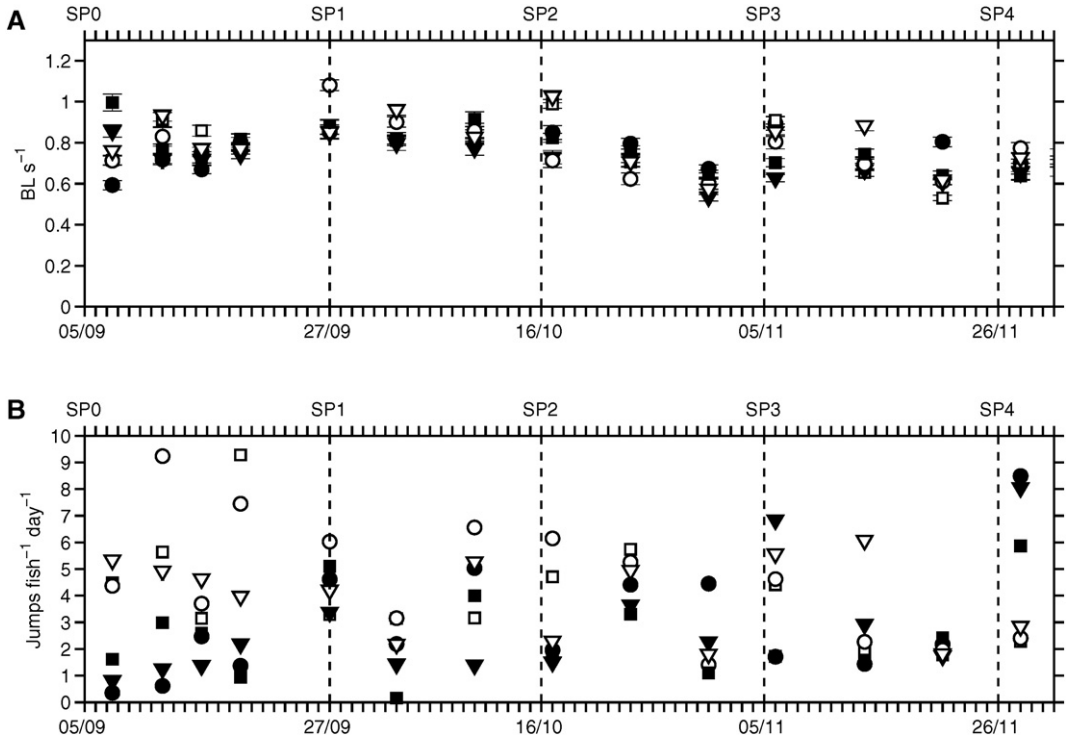

Fig. 6. A) Mean swimming speeds in body lengths per second and B) jumping frequency for the fish in the three control (white symbols) and three snorkel cages (black symbols). The dates of sample points (SP) 0–4 are indicated by vertical hatched lines.

vs. 29%, $p = 0.012$, $z = -2.5$) (Table 1). Percentage fish with fin damage decreased throughout the trial, and at the last sampling the differences in fin condition between the fish in the control sea-cages and the controls were less pronounced (dorsal fin: 60 vs. 52%, $p = 0.048$, $z = -2.0$) (caudal fin: 3 vs. 1%, $p = 0.172$, $z = -1.4$).

3.7. Growth

There was no significant difference in the weight of sampled fish between the snorkel and control cages at sample point 0 (2.35 ± 0.03 vs. 2.33 ± 0.03 kg, $p = 0.64$, $F = 0.21$), sample point 2 (3.40 ± 0.05 vs. 3.30 ± 0.04 kg, $p = 0.13$, $F = 2.31$) and sample point 4 (4.59 ± 0.06 vs. 4.50 ± 0.06 kg, $p = 0.28$, $F = 1.18$). Condition factor also did not differ among snorkel and control cages at any of the three sample points ($p \geq 0.54$, $F < 0.38$). Furthermore, total mortalities recorded over the whole experimental period were similar between snorkel and control cages (108 ± 6 vs. 129 ± 12, $p = 0.23$, $t = 1.51$).

4. Discussion

4.1. Effect of the snorkel on reducing lice infestation depends upon environmental conditions

We have demonstrated that snorkel sea-cages assist harvest-sized salmon to evade lice larvae in the critical autumn production period.

Table 1
Comparison of mean of percentage fish in each cage per treatment (±standard error) with significant snout damages (score > 1), significant dorsal fin damages (score > 3) and significant caudal fin damages (score > 3) for sample points (SP) 0, 2 and 4.

	Snout		Dorsal fin		Caudal fin	
Sampling	Control	Snorkel	Control	Snorkel	Control	Snorkel
SP 0	0 ± 0.0	1 ± 0.7	93 ± 0.3	84 ± 1.8	39 ± 16.0	29 ± 2.9
SP 2	5 ± 2.0	6 ± 0.3	84 ± 2.3	77 ± 4.7	21 ± 2.0	9 ± 2.0
SP 4	21 ± 2.0	31 ± 2.3	60 ± 8.2	52 ± 7.3	3 ± 1.0	1 ± 0.9

The observed lice reductions were not of the same magnitude as documented previously (Oppedal et al., n.d.: 66–84% reduction), but were still substantial (this study: 24–65% reduction). One likely reason for this difference is that newly transferred post-smolts, as used in Oppedal et al. (n.d.), typically swim shallow during the summer months (Oppedal et al., 2011), which would have placed the control fish at high risk of infestation. In contrast, in our experiment, the control fish during the day typically swam at similar depths as the fish in the snorkel cages (Fig. 3). Therefore, for much of the time they would have experienced the same infestation pressure as the fish in the snorkel cages. The effect of deeper swimming by control fish on the difference in lice infestation intensity between the control and snorkel cages is clear in the period before sample point 1 (Fig. 7). Here, a large portion of the fish swam shallower than 4 m depth for most of the period, except for a few days, which coincided with the theoretical time period for when the chalimus 2 stage lice attached. This is the life history stage for which we recorded the smallest effect of the snorkel technology at this sample point.

In the study on behaviour and individual growth rates in snorkel cages by Dempster et al. (n.d)., the snorkel cages did not reduce lice infestation compared to standard cages. This was most likely due to a consistent surface brackish water layer (20–25 ppt) which extended down to the same depth as the roof of snorkel cages at 3 m (Dempster et al., n.d.; Oppedal et al., n.d.). As a consequence, lice probably remained below this layer, rendering the snorkel ineffective. In the current experiment, no consistent brackish water layers lasted more than a few days. The period just before sample point 2, which had the most consistent brackish water (~23 ppt) down to roof depth during the experimental period, did not lead to any decreased effect from the snorkel on the abundance of chalimus 1 lice (Fig. 4B). This effect may not have been evident as each lice life stage lasts for several days and periods of surface brackish water were at most 1–2 days in duration.

While we do not have data on water current and turbulence, periods with turbulence will mix the water column and create more homogenous temperature and salinity conditions, and at the same time transport lice larvae below the snorkel roof at 4 m depth. In the period before sample point 2, the back-calculated infestation times of chalimus

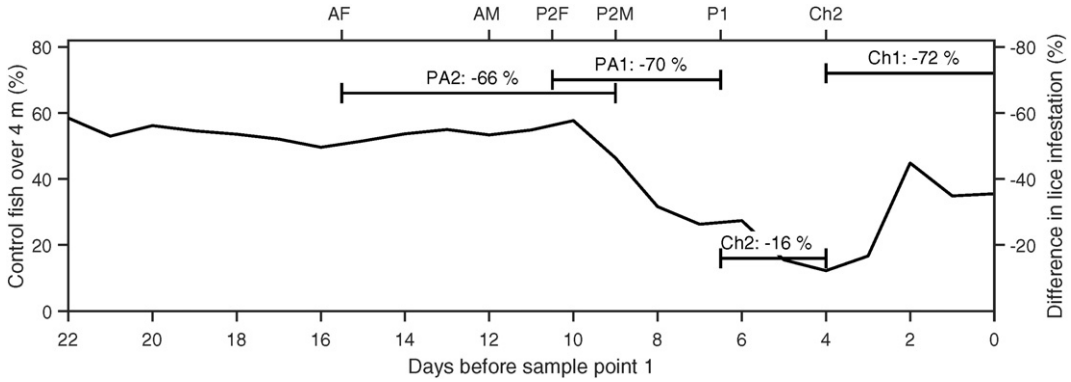

Fig. 7. Effects from the snorkel technology decrease when also the control fish swim deep. Percentage of fish above 4 m in control cages before sample point 1 is represented by the black line (data from Fig. 3A). Back-calculated theoretical moulting times at a temperature of 15 °C (Anonymous, 2009) between specific lice life stages from sample point 1 (Ch2 = moulting from chalimus 1 to chalimus 2, P1 = moulting to pre adult, P2M = moulting to pre adult 2 male, P2F = moulting to pre adult female, AM = moulting to adult male and AF = moulting to adult female) are indicated on the top x-axis. The days for when each classified stage, according to these theoretical moulting times, likely attached are displayed by horizontal bars together with the observed reduction in lice infestation for the respective stage (Ch1, Ch2, PA1 and PA2, data from Fig. 4A).

2 and pre-adult 1 coincided with little stratification in temperature and salinity (Fig. 8). Turbulence may therefore be an explanation for why lice abundance on fish in the snorkel and control cages did not differ for these two stages at sample point 2 (Fig. 4B).

While fish swimming depth in the control cages and mixing of surface water with deeper water should, according to theory, have the effects as shown in the examples (Figs. 7 and 8), the experiment was not designed to test the causality of these relationships. This would have required a series of experiments that accounted for the many stochastic processes that are present. These include environmental stratification (position of halocline and thermocline), position of the fish in the control cages, infestation pressure in the area, and variations in horizontal water current. Despite the observed variability in effect size between control and snorkel cages, the experiment clearly demonstrated that for the majority of the time and in most of the conditions, snorkel cages markedly reduced sea lice infestation levels compared to control cages, demonstrating the potential of the snorkel principle as a method for reducing lice infestation in salmon farming. The effectiveness of snorkel cages could be enhanced by making the snorkel deeper and by combining it with the use of cleaner fish.

4.2. Effects of the snorkel on major production parameters and indicators of welfare

Sea lice create physical damage to their hosts and induce a range of stressful responses and decrease fish welfare (Stien et al., 2013). Reducing lice loads across the experimental periods by 24–65% thus reduced these negative effects on the salmon in snorkel cages. Sea lice often feed on the fins, especially the dorsal fin (Bjørn and Finstad, 1998), and the lower levels of damage to fins in the snorkel cages compared to the control cages at sample points 2 and 4 may be a result of higher lice loads. However, since there was also a difference in fin condition at sample point 0, before the experiment had started, with more fin damage in control cages; an alternate explanation is that sampling influenced how damaged fins were. Fish were easily collected in small nets when they were pulled up through a snorkel, though this method was rougher on the fish when nets were pulled up through a small section of a control cage. Thus, higher netting pressure on control fish may have increased their fin wear relative to snorkel fish. This potential discrepancy in sampling effects between control and snorkel cages indicates that fin data should be interpreted with caution in the current study, and these effects should be carefully considered in future studies.

By feeding to excess, the fish had ready access to feed in both control and snorkel cages and we detected no differences in growth rates. This result, is in-line with the result from Dempster et al. (n.d.) and indicates that once translated to full scale production, snorkel cages should perform similarly to standard cages if feed is properly delivered to the fish within them. The increased level of snout damage observed on the fish in the snorkel cages, as also seen in Dempster et al. (n.d.), is probably a consequence of fish damaging themselves against the net roof or the snorkel itself. This problem may be reduced in commercial-scale snorkel units, with their increased size and hence increased area

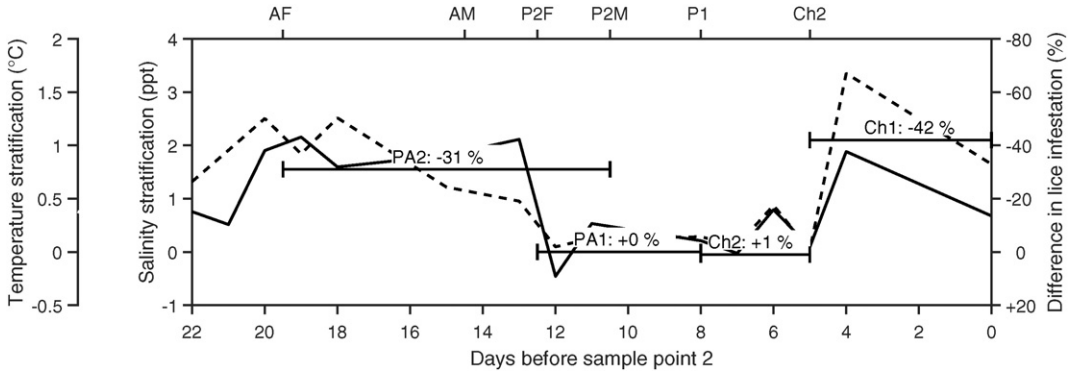

Fig. 8. Effects from the snorkel technology decrease when the environment data indicate that there is mixing of surface and deep water. Difference in temperature, in the period before sample point 2, between 1 and 5 m depth is represented by the black solid line and the difference in salinity by the black hatched line (data from Fig. 2). Back-calculated theoretical moulting times at a temperature of 13 °C (Anonymous, 2009) between specific life stages from sample point 1 (Ch2 = moulting from chalimus 1 to chalimus 2, P1 = moulting to pre-adult, P2M = moulting to pre-adult 2 males, P2F = moulting to pre-adult female, AM = moulting to adult male and AF = moulting to adult female) are presented on the top x-axis. The days for when each classified stage, according to theoretical moulting times, likely attached are indicated by horizontal bars together with the observed reduction in lice infestation for the respective stage (Ch1, Ch2, PA1 and PA2, data from Fig. 4B).

open to the surface, reducing the risk of contact with the sides of the snorkel and the net roof.

When sea-cages are fully submerged and salmon are denied access to the surface to re-fill their swim bladders, the echo sounder signal declines over the a 21 day period, which indicates that fish gradually lose air from their swim bladders and become negatively buoyant (Dempster et al., 2009; Korsøen et al., 2009). Further, when surface access is re-instated after long periods of submergence, a rapid burst in swim bladder re-filling activity occurs (Dempster et al., 2009; Korsøen et al., 2009). The results from the current trial suggests that the fish within the snorkel cages re-filled their swim bladders continuously, as the recorded echo strength maintained values similar to those prior to snorkel installation. In contrast, in Dempster et al. (n.d.), with a lower stocking density (only 1.5 kg m^{-3}) and medium-sized fish (~1.5 kg), echo-sounder values declined to below 50% of starting values, indicating that these fish only partly re-filled their swim bladders (Dempster et al., n.d.), and a slight but significant increase in swimming speeds resulted. In contrast, in this trial swimming speeds did not increase, indicating that fish used the snorkel enough to maintain their buoyancy throughout the entire trial.

The higher rate of surface activity recorded for the control fish may be explained by their unhindered access to the surface, but also their lice loads. Lice infestation leads to more jumping in salmon (Furevik et al., 1993; Samsing et al., 2015; Webster et al., 2007). The strong increase in surface activity for the snorkel cages after full surface access was re-instated could be a consequence of the novelty a newly opened surface space poses after a long period of behavioural restriction due to the roof, and as such, raises a possible welfare concern (Dawkins, 1988).

5. Conclusions, practical implications and future development

Our study highlights the substantial potential for preventing a significant level of sea lice infestation by using snorkel sea-cages on large salmon raised at commercial stocking densities during autumn. There was a substantial reduction in lice infestation and little, or no, adverse effects on fish growth and fish welfare compared to controls. Moving from research to industrial sea-cage scale will mean solving numerous practical and technological challenges, in parallel with testing as to whether salmon can cope in such commercial sized systems. Future research should also assess if snorkels which extend down to greater depth lead to further and more consistent reductions in lice infestation pressure relative to control cages. Deeper snorkels could concurrently reduce surface use by salmon, and thus welfare risks will again need to be assessed.

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References

Anonymous, 2009. Bestemmelsesskjema for lakselus.
Bjordal, Å., Juell, J.-E., Lindem, T., Fernö, A., 1993. Hydroacoustic monitoring and feeding control in cage rearing of Atlantic salmon (*Salmo salar* L.). Fish Farming Technology. Balkema, Rotterdam, pp. 203–208.
Bjørn, P.A., Finstad, B., 1998. The development of salmon lice (*Lepeophtheirus salmonis*) on artificially infected post smolts of sea trout (*Salmo trutta*). Can. J. Zool. 76, 970–977.
Crawley, M.J., 2012. The R Book. John Wiley & Sons.
Dawkins, M.S., 1988. Behavioural deprivation: a central problem in animal welfare. Appl. Anim. Behav. Sci. 20, 209–225.
Dempster, T., Juell, J.-E., Fosseidengen, J.E., Fredheim, A., Lader, P., 2008. Behaviour and growth of Atlantic salmon (*Salmo salar* L.) subjected to short-term submergence in commercial scale sea-cages. Aquaculture 276, 103–111.
Dempster, T., Korsøen, Ø., Folkedal, O., Juell, J.-E., Oppedal, F., 2009. Submergence of Atlantic salmon (*Salmo salar* L.) in commercial scale sea-cages: a potential short-term solution to poor surface conditions. Aquaculture 288, 254–263.
Dempster, T., Bui, S., Stien, L.H., Oppedal, F., (n.d.) Effects of the cage-based "snorkel" sea lice barrier technology on Atlantic salmon growth, condition and behaviour. (Data not publish, article under review)
Frank, K., Gansel, L.C., Lien, A.M., Birkevold, J., 2015. Effects of a Shielding Skirt for Prevention of Sea Lice on the Flow Past Stocked Salmon Fish Cages. J. Offshore Mech. Arct. Eng 137, 011201.
Frenzl, B., Stien, L.H., Cockerill, D., Oppedal, F., Richards, R.H., Shinn, A.P., Bron, J.E., Migaud, H., 2014. Manipulation of farmed Atlantic salmon swimming behaviour through the adjustment of lighting and feeding regimes as a tool for salmon lice control. Aquaculture 424-425, 183–188.
Fulton, T.W., 1904. The rate of growth of fishes. Annu. Rep. Fish. Res. Board Scotl. 22, 141–241.
Furevik, D.M., Bjordal, Å., Huse, I., Fernö, A., 1993. Surface activity of Atlantic salmon (*Salmo salar* L.) in net pens. Aquaculture 110, 119–128.
Grøntvedt, R.N., Jansen, P.A., Horsberg, T.A., Helgesen, K., Tarpai, A., 2014. TThe surveillance programme for resistance to chemotherapeutants in *L. salmonis* in Norway. Surveillance Programmes for Terrestrial and Aquatic Animals in Norway. Annual Report 2013. Norwegian Veterinary Institute, Oslo.
Hamre, L.A., Eichner, C., Caipang, C.M.A., Dalvin, S.T., Bron, J.E., Nilsen, F., Boxshall, G., Skern-Mauritzen, R., 2013. The Salmon Louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) life cycle has only two Chalimus stages. PLoS One 8, e73539.
Helgesen, K.O., Romstad, H., Aaen, S.M., Horsberg, T.E., 2015. First report of reduced sensitivity towards hydrogen peroxide found in the salmon louse *Lepeophtheirus salmonis* in Norway. Aquac. Rep. 1, 37–42.
Heuch, P.A., Parsons, A., Boxaspen, K., 1995. Diel vertical migration: a possible host-finding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids? Can. J. Fish. Aquat. Sci. 52, 681–689.
Hevrøy, E., Boxaspen, K., Oppedal, F., Taranger, G., Holm, J., 2003. The effect of artificial light treatment and depth on the infestation of the sea louse *Lepeophtheirus salmonis* on Atlantic salmon (*Salmo salar* L.) culture. Aquaculture 220, 1–14.
Hoyle, I., Oidtmann, B., Ellis, T., Turnbull, J., North, B., Nikolaidis, J., Knowles, T.G., 2007. A validated macroscopic key to assess fin damage in farmed rainbow trout (*Oncorhynchus mykiss*). Aquaculture 270, 142–148. http://dx.doi.org/10.1016/j.aquaculture.2007.03.037.
Iversen, A., Hermansen, Ø., Andreasen, O., Brandvik, R.K., Marthinussen, A., Nystøyl, R., 2015. Kostnadsdrivere i lakseoppdrett. Trondheim: Sintef: Rapport 41/2015.
Johannessen, A., 1977. Early stages of *Lepeophtheirus salmonis* (Copepoda, Caligidae). Sarsia 63, 169–176.
Johansson, D., Laursen, F., Fernö, A., Fosseidengen, J.E., Klebert, P., Stien, L.H., Vågseth, T., Oppedal, F., 2014. The interaction between water currents and salmon swimming behaviour in sea cages. PLoS One 9, e97635.
Johnson, S.C., Albright, L.J., 1991. Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. J. Mar. Biol. Assoc. U. K. 71, 425.
Jones, S., Beamish, R., 2011. Salmon Lice: An Integrated Approach to Understanding Parasite Abundance and Distribution. John Wiley & Sons.
Korsøen, Ø.J., Dempster, T., Fjelldal, P.G., Oppedal, F., Kristiansen, T.S., 2009. Long-term culture of Atlantic salmon (*Salmo salar* L.) in submerged cages during winter affects behaviour, growth and condition. Aquaculture 296, 373–381.
Korsøen, Ø.J., Fosseidengen, J.E., Kristiansen, T.S., Oppedal, F., Bui, S., Dempster, T., 2012. Atlantic salmon (*Salmo salar* L.) in a submerged sea-cage adapt rapidly to re-fill their swim bladders in an underwater air filled dome. Aquac. Eng. 51, 1–6.
Murray, A.G., 2014a. A modelling framework for assessing the risk of emerging diseases associated with the use of cleaner fish to control parasitic sea lice on salmon farms. Transbound. Emerg. Dis. http://dx.doi.org/10.1111/tbed.12273.
Murray, A.G., 2014b. A note on sea lice abundance on farmed Atlantic salmon in Scotland 2011–2013: significant regional and seasonal variation. Aquac. Res. 47, 961–968.
Næs, M., Heuch, P.A., Mathisen, R., 2012. Bruk av «luseskjørt» for å redusere påslag av lakselus *Lepeophtheirus salmonis* (Krøyer) på oppdrettslaks.
Ona, E., 1990. Physiological factors causing natural variations in acoustic target strength of fish. J. Mar. Biol. Assoc. U. K. 70, 107.
Oppedal, F., Dempster, T., Stien, L.H., 2011. Environmental drivers of Atlantic salmon behaviour in sea-cages: a review. Aquaculture 311, 1–18.
Oppedal, F., Dempster, T., Bui, S., Stien, L.H., n.d. Mismatching host and parasite environments reduces encounter rates and prevents infestation of farmed salmon by sea lice. (Data not publish, article under review)
Samsing, F., Solstorm, D., Oppedal, F., Solstorm, F., Dempster, T., 2015. Gone with the flow: current velocities mediate parasitic infestation of an aquatic host. Int. J. Parasitol. 45, 559–565.
Saunders, R.L., 1965. Adjustment of buoyancy in young Atlantic Salmon and Brook trout by changes in swimbladder volume. J. Fish. Res 22, 335–352. http://dx.doi.org/10.1139/f65-034 (Board Canada).
Stien, L.H., Nilsson, J., Hevrøy, E.M., Oppedal, F., Kristiansen, T.S., Lien, A.M., Folkedal, O., 2012. Skirt around a salmon sea cage to reduce infestation of salmon lice resulted in low oxygen levels. Aquac. Eng. 51, 21–25.
Stien, L.H., Bracke, M.B.M., Folkedal, O., Nilsson, J., Oppedal, F., Torgersen, T., Kittilsen, S., Midtlyng, P.J., Vindas, M.A., Øverli, Øyvind, Kristiansen, T.S., 2013. Salmon Welfare

Index Model (SWIM 1.0): a semantic model for overall welfare assessment of caged Atlantic salmon: review of the selected welfare indicators and model presentation. Rev. Aquac. 5, 33–57.
Strand, I.M., Soerensen, A., Lader, P., Volent, Z., 2013. Modelling of drag forces on a closed flexible fish cage. Control Applications in Marine Systems, pp. 340–345.
Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O.T., Nilsen, F., Horsberg, T.E., Jackson, D., 2013. Salmon lice-impact on wild salmonids and salmon aquaculture. J. Fish Dis. 36, 171–194.
Treasurer, J., Feledi, T., 2014. The physical condition and welfare of five species of wild-caught wrasse stocked under aquaculture conditions and when stocked in Atlantic Salmon, *Salmo salar*, Production Cages. J. World Aquacult. Soc. 45, 213–219.
Webster, S.J., Dill, L.M., Butterworth, K., 2007. The effect of sea lice infestation on the salinity preference and energetic expenditure of juvenile pink salmon (*Oncorhynchus gorbuscha*). Can. J. Fish. Aquat. Sci. 64, 672–680.