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Full production cycle, commercial scale culture of salmon in submerged sea-cages with air domes reduces lice infestation, but creates production and welfare challenges

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ABSTRACT

Structural modification of sea cages is continually changing to counter major production issues associated with commercial salmon farming. For example, snorkels and skirts are added to cages to reduce salmon lice infestations, and submerging cages can reduce salmon-lice encounter rates, minimise the effects of storms or avoid other unsuitable sea surface conditions. Unlike snorkels and skirts, the uptake of submerged cages has stalled due to negative effects associated with salmon buoyancy, as salmon require frequent access to the surface to gulp air and fill their swim bladders. Fitting submerged cages with underwater air domes provides an underwater air surface and appears to resolve buoyancy associated issues, but they have not been tested over a full production cycle. Here, we used three 1728 m^3 cages submerged to 15 m fitted with air domes and three standard surface cages (i.e. control cages) to grow ~6000 fish per cage from sea transfer (~ 0.2 kg) to harvest size (~5 kg). We tested if growth rates, swimming behaviour, key SWIM (Salmon Welfare Index Model) welfare parameters and lice infestation levels differed between control and submerged cages. Submerged cages had 93% lower lice levels than controls during a large lice pulse event in mid-winter, which was visible through the subsequent lice stages. Swim bladder fullness, swimming behaviour and surface activity rates indicated submerged fish competently used the underwater airdome to maintain neutral buoyancy for the full production cycle. However, after 12 months, harvested mean fish weight was far smaller in submerged (2.8 kg) than control (5 kg) cages and overall mortality 2.5 times higher. Likewise, SWIM welfare scores for eye condition and mouth jaw wounds were worsened in submerged than control cages. The poorer outcomes in submerged cages reflect the suboptimal environmental conditions experienced deeper in the water column, where colder water and/or lower oxygen levels for long periods may have compromised growth. We conclude that while submergence can reduce lice infestation rates, strategies to do so must ensure that fish do not encounter sub-optimal environments for fish growth and welfare.

1. Introduction

The salmon aquaculture industry has recently begun to move towards more preventative lice control techniques rather than lice treatment methods, through improving sea cage farming practice (see review by Barrett et al., 2020a). Modifying the physical structure of sea cages is a pro-active way to help prevent lice numbers on salmon in sea cages exceeding allowable threshold limits. For example, the installation of tarpaulin skirts (Stien et al., 2018; Grøntvedt et al., 2018; Bui et al., 2020) or snorkels (Stien et al., 2016; Oppedal et al., 2017, 2019; Wright et al., 2017, 2018; Geitung et al., 2019) that create a physical barrier between salmon in sea cages and salmon lice that mainly reside in surface waters (Johannessen, 1978; Costelloe et al., 1995; McKibben and Hay, 2004; Oppedal et al., 2017) is becoming more widely used by the Norwegian salmon industry to prevent excessive sea lice infection.

An alternative lice prevention method is to submerge cages and create a depth-based spatial barrier between salmon and salmon lice (Sievers et al., 2018; Oppedal et al., 2020). Submerging cages may also

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provide additional benefits by being less susceptible to storms, wave damage events, net deformations from strong currents, algal or jellyfish blooms, toxic aluminium levels in brackish waters above the halocline, and biofouling (Dempster et al., 2009). Furthermore, during summer months, high surface temperatures alone or in combination with increased oxygen demand (Hvas et al., 2017) may increase the occurrence of poor oxygen conditions (Solstorm et al., 2018; Burke et al., 2021) above or below the thermocline, leading to poorer growth (Remen et al., 2016; Wade et al., 2019) or higher mortalities for Atlantic salmon held in standard surface sea cages. Similarly, low surface temperatures in winter are regularly seen, with warmer conditions at depth (e.g. Bui et al., 2020). Hence, submerging cages could counteract the effect of sub-optimal surface temperatures in summer or winter by ensuring fish are held deeper, in more optimal conditions for growth and survival.

For submerged cage farming to succeed, fish must be able to maintain normal buoyancy and swimming behaviour during submergence. Full scale production using submerged sea cages is now feasible for physoclist finfish species such as European sea bass and Atlantic cod that regulate buoyancy through a closed swim bladder (Maricchiolo et al., 2011; Chambers and Howell, 2006) and cobia, that have no swim bladder for buoyancy regulation (Benetti et al., 2010). Regulating buoyancy for the physostomous Atlantic salmon is more complicated as they have an open swim bladder that requires salmon to be able to access the surface to refill with air (Dempster et al., 2009; Korsøen et al., 2009). Recent advances in submerged cage technology enable this to occur via the addition of an underwater air dome (Korsøen et al., 2012; Oppedal et al., 2020). When an air dome was added to a submerged cage for 5–7 weeks holding 0.5–1.5 kg salmon, there was little to no short-term effects of submergence on salmon swim behaviour, buoyancy, welfare, and growth (Oppedal et al., 2020). However, the long-term effects of submerging salmon for a full sea-cage production cycle requires testing before the industry may adopt submerged cages. Short-term submergence (7 weeks) can greatly reduce the levels of the infective attached stages of lice (Sievers et al., 2018). But, whether submergence for a full production cycle can limit infestations of adult lice below allowable threshold limits remains unknown (e.g. 0.5 adult female lice fish^{-1} in Norway, Norwegian Ministry of Trade and Fisheries, 2012). Furthermore, documentation of good welfare and normal behaviour during long-term submergence is required, such as normal swim speeds, refilling activity and vertical distribution, and good external appearance, growth, and condition.

Here, we tested the viability of using submerged cages fitted with air domes at an industry relevant scale over a full sea-cage production cycle. Three submerged cages fitted with octagonal air domes and three standard surface cages (i.e. control cages) were used to grow Atlantic salmon from smolts through to harvest. Between cage types, we compared salmon growth, swimming behaviour, relevant key SWIM (Salmon Welfare Index Model, Stien et al., 2013) welfare parameters, and natural lice infestation loads over a period of 12 months.

2. Methods

2.1. Animal ethics

All fish handling and rearing complied with the Norwegian animal welfare act and was approved by the Norwegian Animal Research Authority (permit no.19629).

2.2. Submerged cage and air dome set-up

Sea cage production of Atlantic salmon was conducted from June 2019 to June 2020 at the Cage Environment Laboratory within the Institute of Marine Research sea facility at Smørdal, Masfjorden, Norway (60°N). Masfjorden is a typical fjord salmon farming site with a strong pycnocline. Control cages ($n = 3$) were open to the surface with the bottom weight line of the cage set to a depth of 12 m (12 m × 12 m × 12 m deep; total volume ~ 1728 m^3). Submerged sea cages (n = 3) of the same dimensions as controls were fitted with a 2.5 m diameter octagonal air dome (Plastinvent, surface area ~ 4.9 m^2, air pocket apex height 0.1 m). The net ceiling was set at 15 m deep and bottom weight line at 27 m. All cages were positioned in a row perpendicular from land with alternating replicates of control and treatment cages. The main water current direction flowed parallel to the shore with minimum water interactions between cages. One week prior to the start of the trial, cages were stocked with ~6000 naive Atlantic salmon (Aquagen strain) (Supp table. 1) that ranged from 200 to 300 g in weight. Domes were added to the three treatment cages over a one-week period starting 21st June 2019 and removed 15-18th June 2020.

Fish were fed (spirit S 75-50A3, Spirit 4.5 mm Nutra and Premium 4.5, 7, 1200 pellet size according to fish size, Skretting, Norway) to apparent satiation (waste feed present under the fish during the last meal of the day) adjusted 3 days per week over the 12-month trial. Feed delivery times were between 06:45 and 15:00, adjusted to start at 08:45 in winter darkness and then to 05:30 from May 2020 onwards. Control fish were fed directly via the surface using a commercial central feed system (Steinsvik, steinsvik.no) that blows the feed to the individual cage and scatters it with a small spreader attached at the pipe end. Fish in submerged cages had feed blown out with the same system, but instead of using a small spreader at the pipe end, for each cage, feed was transferred into a pipe (Ø = 190 mm) that was submerged to a depth of 6 m to direct the pellets downwards. For the first 5 months (October 2019) feed delivered via the submerged pipe passively descended through the net ceiling to the fish. After October 2019, due to the next pellet size (1200) being too big to pass through the mesh of the net ceiling, the delivery pipes for submerged cages were extended to 18.8 m so that the end penetrated the net ceiling to deliver feed directly to the submerged fish. Horizontal pellet spreading from the extended pipe was limited. Feeding was stopped for 1–3 days prior to each sampling date, and on the 14 June 2020 in preparation for the final sampling and slaughter. Submerged light sources (Blue led light 400 W, www.akvagroup.com) were turned on from 28 February 2020 onwards, in an attempt to mitigate increased mouth wounds observed in all cages. These were positioned at 8 m below the sea surface only in the dome cages and thus providing similar intensity to fish in dome cages 8+ m below and the control cage 8+ m sideways.

1200 cleaner fish, lumpfish *Cyclopterus lumpus* (~ 0.1 to 0.3 kg) were added to each cage in February 2020 as a continuous treatment to keep lice levels low. Lumpfish eat large adult lice, and often preadult stages (Imsland et al., 2014, 2018). Daily mortalities of lumpfish were registered and accumulated mortality by the end of June 2020 was 60 ± 20% in control cages and 66 ± 17% in submerged cages (mean ± SD).

2.3. Environment

Temperature, salinity, and dissolved oxygen levels in the fjord was monitored by an automatic profiling buoy (APB5, SAIV A/S, Bergen, saiv.no) positioned at the outer end of the farm, profiling two times a day from 0 to 40 m depth.

2.4. Fish condition, welfare and growth

Day 1 of the trial was on the 21st June 2019 at which time 30 fish were sampled from each cage either using a hoop net or small dead-fish net (both ~1 m in diameter) to obtain an initial welfare assessment using the Salmon Welfare Index Model for skin, fin, mouth jaw wounds and eye condition (SWIM: Stien et al., 2013). Low SWIM scores indicate better fish condition and higher SWIM scores poorer condition. Index scores range from 1 to 7 for skin, 1 to 4 for fin and mouth jaw wounds, and 1 to 5 for eye condition. Detailed descriptions of each welfare index score used is described in Stien et al., (2013). In addition to SWIM scores estimates of fish length, weight, condition, and number of lice at all stages (sessile copepodids, chalimus I and II; mobile preadult I and II,

adult males and females) were taken. Each submerged cage was raised to the same height as the control cages in the 2 h prior to being sampled. Sampling of 30 fish per cage was repeated approximately every 8 weeks throughout to enable comprehensive monitoring of fish health during complete grow-out. From the 4th sample date onwards (December 2019 to June 2020) a larger hoop net was used to sample fish (~2 m diameter) due to the increase in fish size. Final samples were taken 21–24 June 2020, only 4 weeks after the previous. Commercial harvest data (gutted weights and fillet quality) was only available for the combined total number of fish from all replicate cages within each treatment type. Mortalities from each cage were removed and registered daily.

2.5. Behavioural observations

2.5.1. Swim bladder refilling in the dome

For each submerged cage, camera and video observations were used to assess whether salmon surfaced inside the dome area. A fixed camera with an infra-red light (WCAM-50IR, Smartprodukter, Ulsteinvik, Norway) was mounted inside the dome to observe the surface layer and a pan-tilt camera mounted on a profiling winch (ORBIT 3500, ScaleAQ, Førresfjorden, Norway) positioned next to and under the dome. Swim bladder refilling activity in the dome was observed for 5 min during the daytime approximately every 3rd or 4th day via the camera inside the dome aided by simultaneous observation with the pan-tilt camera. When the head of a salmon broke the surface, which occurs during both rolling and jumping behaviour (Dempster et al., 2009), this was considered a swim bladder refilling attempt.

2.5.2. Swimming speeds

Swim speed observations, taken approximately every 3rd or 4th day, were calculated as body lengths per second (BL s^{-1}) by measuring the time taken for the snout and then the caudal fin to pass a vertical reference line within the cage and calculating the inverse number (Dempster et al., 2008). Speeds were recorded for a total of 30 randomly chosen individuals: 15 individuals while the camera was facing North and 15 when facing South to account for any difference in speed based on water current direction (predominantly West or East bounding).

2.5.3. Swimming depth and relative echo strength

Swimming depth distributions of fish in the control and submerged 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 ~17 m depth (control cages) or ~ 32 m (submerged cages) facing upwards with a 42° acoustic beam. Using the detailed, vertical behaviour, depth distribution and total echo strength (Stien et al., 2016) for each cage (Supp Fig. 1-6), average fish depth and relative echo strength were summarized into estimated weekly means for the three submerged and three control cages (± 1 standard deviation) to enable a clear comparison to environmental data recorded over the trial period and swim bladder fullness. Weekly relative echo strength

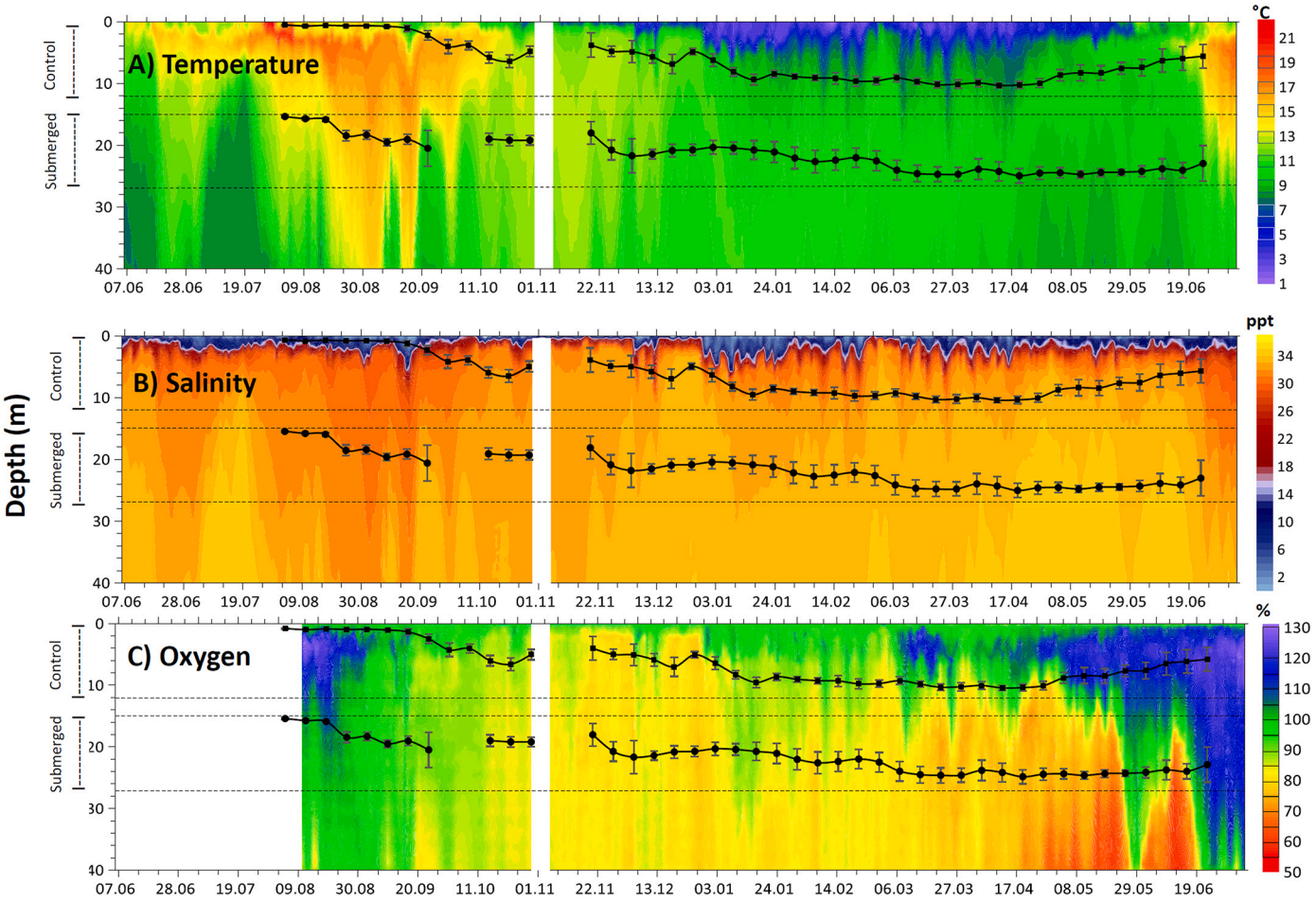

Fig. 1. Temperature (A), salinity (B) and dissolved oxygen (C) (% saturation) measured in the Masfjorden during the 12-month submergence trial, June 2019 to June 2020. Dashed lines —— indicate approximate position of the bottom of surface cage (@12 m deep), net ceiling of submerged cage (@15 m deep), and bottom of submerged cage (@27 m deep). Black squares indicate weekly mean position (± 1 SD) of fish in the 3 control cages, black circles weekly mean position (± 1 SD) of fish in the 3 submerged cages. White areas in environmental parameters and non-connecting black lines for fish depth, indicate lack of data.

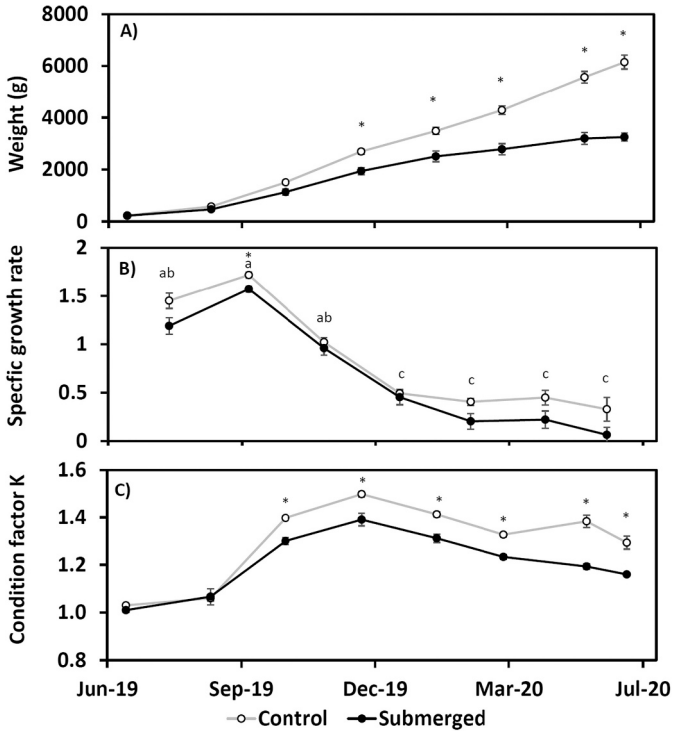

Fig. 2. Average weight gain (A), specific growth rate (B), and condition factor K (C) during sea cage grow out in 3 standard surface cages (Control) compared to 3 submerged cages fitted with an underwater airdome (Submerged). Error bars are ±1 SE. Different letters denote significant differences over time, and * between treatment groups when $p < 0.05$.

was calculated for each individual cage by dividing the weekly total echo strength by the average total echo strength for the cage from the whole trial period × 100 and expressed as a %. Weeks where cage sampling occurred were excluded to remove any effects of disturbance due to sampling, influencing the whole trial average total echo strength value for a given cage.

2.5.4. Surface activity following net ceiling removal and reinstatement of surface access

Net ceilings were removed from submerged cages during the daytime (between 09:00 and 15:00) and the bottom of the cages raised to the same depth as control cages prior to final sampling and harvested. Surface activity in the form of rolling and jumping behaviour (Dempster et al., 2008) was monitored for a period of 5 mins every 30 mins starting one hour prior to removing net ceilings from submerged cages and during the follow 3½ hours post net ceiling removal. Surface activity in control cages were also monitored for 5 min every 30 mins over a 5-h period within the same daytime period to allow for a direct comparison.

2.6. Statistical analysis

Salmon weight, specific growth rate (SGR), condition factor K, SWIM scores (skin, fin, eye, mouth jaw condition), sessile lice (copepodite, chalimus stages I and II) and mobile lice stages (Pre adult I and II and adult male and females) were compared between the submerged and control cages using a series of Mixed design ANOVAs (Repeated measures (RM) and simple main effects (SM)). To estimate infestation level, sessile lice stages (chalimus stages I and II,) were back calculated from the time of sampling to the midpoint of their infestation date based on stages using their estimated temperature-dependent development rate (Hamre et al., 2019) for the period January to mid-June 2020. For back calculations, it was assumed that fish would reside in the most preferred optimal temperature conditions, which for this period was estimated to be 11 degrees.

For all repeated measures analysis, in cases where the interaction term was non-significant, but there was a main effect of time, significant changes over time were compared using pairwise comparisons with a Bonferroni correction and are depicted by different letters above each time point in figures. For significant interactions and main effects of cage type, significant differences between control and submerged cages at a given time point, analysed using simple main effects, are depicted by a * above the associated time point on figures. Analysis of lice counts were only conducted from December 2019 to June 2020, as minimal lice were observed prior to December 2019. Lice counts were square root transformed to meet sphericity assumptions for repeated measures ANOVAs. Cumulative mortality, surface activity, and SWIM scores recorded over the 12-month sea cage period, and surface activity measured at harvest, were analysed using Mixed design ANOVAs as per

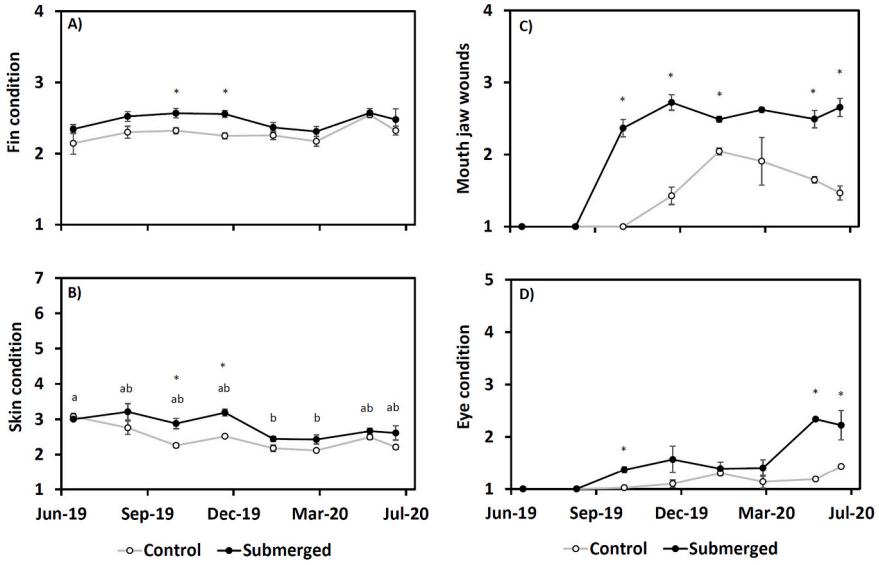

Fig. 3. Average SWIM scores for fin condition (A), skin condition (B), mouth jaw wounds (C) and eye condition (D) at each sampling date during sea cage grow out in 3 standard surface cages (Control) and 3 submerged cages, each fitted with an underwater airdome (Submerged). Error bars are ±1 SE. Higher scores (Y axis) indicate increase in severity of condition.

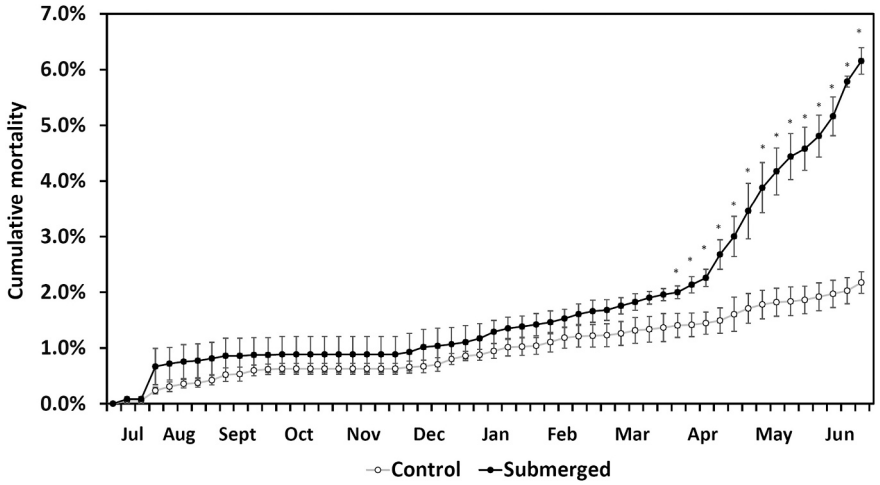

Fig. 4. Average weekly cumulative mortality of fish during sea cage grow out (July 2019 to June 2020) in 3 standard surface cages (Control) and 3 submerged cages, each fitted with an underwater airdome (Submerged). Error bars are ±1 SE. (*) represents weeks were there is a significant difference between submerged and controls when $p < 0.05$.

above. Greenhouse Giesser (GG) corrected test values are reported for all repeated measures tests when there were > 5 time points, or when data failed Mauchly's test of sphericity. For all tests, the significant difference level was set at $p < 0.05$. All analyses were conducted using SPSS 26 statistical software package.

3. Results

3.1. Environment

Temperature followed a normal seasonal pattern with warmest waters at the surface in the summer and autumn and at depth in winter months (Fig. 1a). Salinity displayed a typical fjord pattern with a brackish surface water layer reaching at most 5 m down and with full salinity oceanic below (Fig. 1b). Oxygen conditions in the upper 5–12 m were above 80% saturation for the entire trial and below 15 m deep until November 2019 (Fig. 1c). Below 15 m after November 2019, lower values (70–80% saturation) occurred during winter, decreasing further (consistently <75% saturation) from March 2020 onwards.

3.2. Fish production parameters

3.2.1. Weight

At the beginning of the trial in June 2019, fish weights were similar in control (mean ± S.D. = 230 ± 15 g) and submerged cages (220 ± 29 g). Over the 12-month grow out period, there was an interaction between time and cage type for weight (RM time*cage: $F_{GG\ 2.3,9.0} = 58$, $p < 0.001$). By December 2019, control fish were 1.4 times heavier than submerged fish (SM Dec 2019: $F_{1,5} = 20$, $p = 0.01$), and by mid-June 2020, two weeks prior to harvest, control fish were 1.9 times heavier than submerged fish (SM Jun 2020: $F_{1,5} = 87$, $p < 0.001$, Fig. 2a).

3.2.2. Specific growth rate

SGRs depended on time (RM time: $F_{GG\ 2.3,8.8} = 107$, $p < 0.001$) and cage type (RM cage: $F_{1,4} = 131$, $p < 0.001$) with no significant interaction (RM time*cage: $F_{GG\ 2.3,8.8} = 0.73$, $p = 0.6$). On average the SGRs in control fish were 30% better than submerged fish for the 12-month grow out period (Fig. 2b). SGRs for both submerged and control fish were initially greater than 1.2 and peaked in October 2019 with control fish having a higher SGR than submerged fish (SM Oct 2019: $F_{1,5} = 12$, $p = 0.0.03$) before all fish experienced even levels and a decline in SGRs over winter to stabilise around and below 0.5 from February 2020 till the end of the trial (Fig. 2b).

3.2.3. Condition factor K

Initial condition factor K was similar between control and submerged fish (Jun 2019, 1.03 ± 0.01 & 1.01 ± 0.02, respectively). Over the grow out period, there was an interaction between time and cage type for fish condition (RM time*cage: $F_{GG\ 2.9,11.4} = 8.7$, $p = 0.003$). By October 2019, control fish were in 7% better condition than submerged fish (SM Oct 2019: $F_{1,5} = 30$, $p = 0.01$), which increased to 11% better condition by mid-June 2020, two weeks prior to harvest (SM June 2020: $F_{1,5} = 23$, $p < 0.01$, Fig. 2c).

3.2.4. Commercial harvest data

At the end of the trial, fish were sent to a commercial processor on the 2nd July 2020. 14,845 fish were processed from the three control cages, returning a bled and gutted weight of 74,172 kg (mean fish weight = 5 kg), of which 92% was consider of superior quality. For the three submerged cages, a total of 16,765 fish were processed, returning a bled and gutted weight of 46,053 kg (mean fish weight = 2.8 kg), of which 81% was consider of superior quality.

3.3. Fish welfare

3.3.1. Fin condition

Fin scores ranged from 2.3 to 2.6 and 2.1 to 2.5 for submerged and control fish, respectively, across sampling dates. There was no interaction between cage type and time (RM time*cage: $F_{GG\ 2.5,10.1} = 0.6$, $p = 0.6$) or main effect of time (RM time: $F_{GG\ 2.5,10.1} = 3.8$, $p = 0.05$). There was an effect of cage type (RM cage: $F_{1,4} = 17$, $p = 0.02$) indicating fin condition scores were worse for fish in submerged cages compared to fish in control cages at the October (SM Oct 2019: $F_{1,5} = 8.7$, $p = 0.04$) and December sampling dates (SM Dec 2019: $F_{1,5} = 24$, $p < 0.01$, Fig. 3a).

3.3.2. Skin condition

Scores for skin condition ranged from 2.2 to 3.1 for control fish and 2.6 to 3 for submerged fish over the 12-month grow out period. There was no interaction between cage type and time (RM time*cage: $F_{GG\ 2.8,11.4} = 2.4$, $p = 0.12$). But skin condition did change over time (RM time: $F_{GG\ 2.8,11.4} = 14.7$, $P < 0.001$, Fig. 3b), improving in February and March 2020 relative to the start of the trial, but this improvement had dissipated by the end of the trial (Fig. 3b). A main effect of cage type (RM cage: $F_{1,4} = 9.8$, $p = 0.01$) found that skin condition of control fish were significantly better than submerged fish for the October and December 2019 sampling dates only (SM Oct 2019: $F_{1,5} = 15.6$, $p = 0.02$, SM Dec

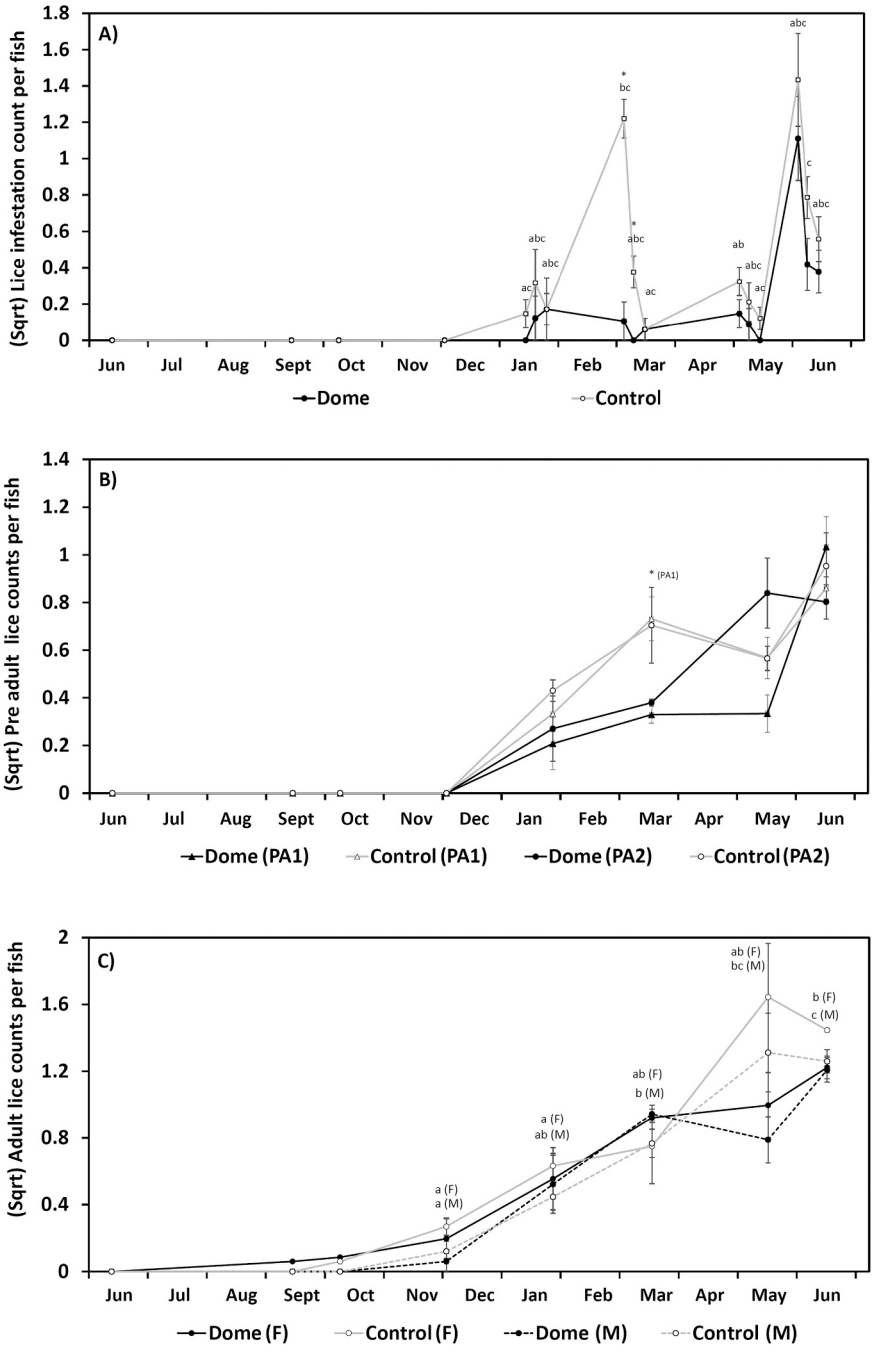

Fig. 5. Lice levels during sea cage grow out in 3 standard surface cages (Control) and 3 submerged cages, each fitted with an underwater airdome. Initial infection rate per fish estimated by back calculating mean infection dates from sessile stages (copepods, chalimus I and II) at each sampling date (A). Mobile stages, pre-adult I and II (B) and adult male and female stage (C). Error bars are ±1 SE. Different letters denote significant differences over time, and (*) differences between treatment groups when $p < 0.05$.

2019: $F_{1,5} = 37$, $p < 0.01$, Fig. 3b).

3.3.3. Mouth jaw wounds

No fish showed signs of mouth jaw wounds in the control or submerged fish during the first two sample dates of the trial (June and August 2019). The occurrence of mouth jaw wounds was first observed in the submerged cages in October 2019 and in December 2019 for control cages. There was an interaction between time and cage type indicating a greater increase in mouth jaw wounds in submerged fish compared to controls as the trial progressed (RM time*cage: $F_{GG\ 2.1,8.5} = 12.8$, $p = 0.003$, Fig. 3c). Mouth jaw wound SWIM scores were worse in submerged fish compared to control fish from October 2019 (SM Oct 2019: $F_{1,5} = 128$, $p < 0.001$). By mid-June 2020, the mean mouth jaw wound SWIM score for submerged fish was 1.8 times worse than control fish (SM Jun 2020: $F_{1,5} = 56$, $p = 0.002$, Fig. 3c).

3.3.4. Eye condition

Deterioration in eye condition occurred by October 2019 with fish in submerged cages deteriorating more quickly over the grow out period compared to fish in control cages (RM time*cage: $F_{GG\ 2.0,7.9} = 7.1$, $p = 0.02$). By October 2019, eye condition differed between submerged and control fish (SM Oct 2019: $F_{1,5} = 31$, $p = 0.005$), but then eye condition was similar over the winter months until March 2020, after which deterioration in eye condition in submerged fish occurred (Fig. 3d). At the final sampling date in mid-June 2020, eye condition scores for submerged fish were 1.6 times worse than for control fish (SM Jun 2020, $F_{1,5} = 7.9$, $p = 0.049$).

3.3.5. Mortality

Total mortality by the end of the trial was 2.5 times higher in submerged cages than control cages. An interaction between time and cage

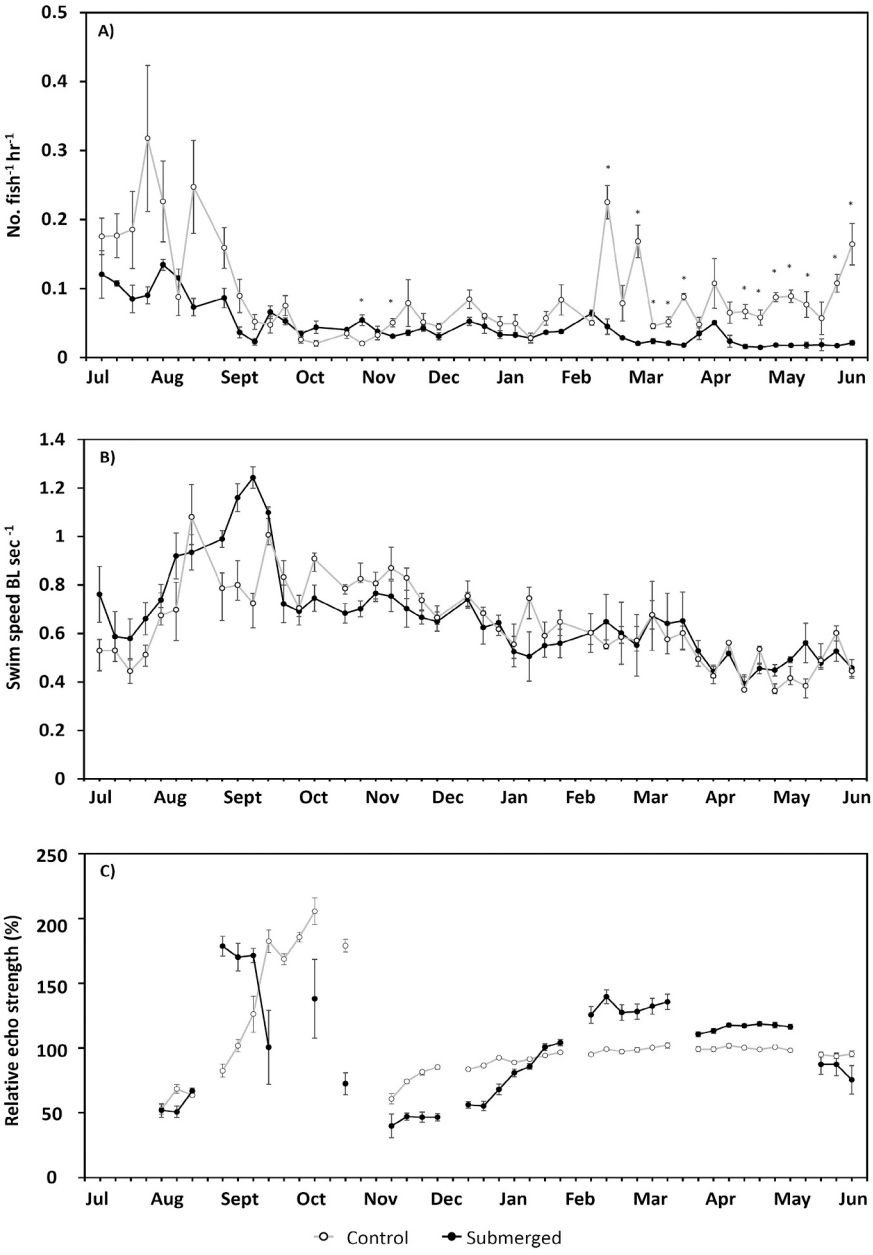

Fig. 6. Surface activity (A), swim speeds (B) and swim bladder fullness (C) of Atlantic salmon from 3 submerged cages (closed circles) and 3 surface access (control) cages (open circles) during sea cage grow out (July 2019 to June 2020). For surface activity (A) each data point represents the weekly average number of surface breaks fish^{-1} h^{-1} ± SE and for swim speeds (B) the weekly average body lengths per second (BL s^{-1}, ± SE). No samples were taken during weeks 8, 16, 24 and 32. (*) represents weeks were there is a significant difference between submerged and controls when $P < 0.05$. Swim bladder fullness (C) is measured as relative echo strength and each data point represents the weekly relative echo strength ± SE for control and submerged cages. Non-connecting black lines between weeks indicate lack of echo sounder data, or weeks when cage sampling occurred.

type (RM time*cage: $F_{GG\ 2.5,9.9} = 24$, $p < 0.001$) indicated cumulative mortality increased at a faster rate from late March 2020 onwards in submerged cages compared to control cages. Cumulative mortality was higher in submerged cages by the week ending March 23rd, 2020 and remained higher for the final 14 weeks (SM cage final 14 weeks, submerged > control $F_{1,5} = 8$ to 217, $P < 0.05$ for all, Fig. 4). 68% of all fish mortalities in submerged cages over the 12-month grow out period occurred in the last 14 weeks of the trial. During this period, 137 dead fish were macroscopically examined and 124 displayed typical signs of *Tenacibaculum* sp. Microbiological and histological analyses of 15 dead fish (Pharmaq Analytic, Bergen, Norway) verified the occurrence of *Tenacibaculum* sp. along with other systemic bacteria such as *Aliivibrio wodanis*, *Vibrio splendius* and *Vibrio tapetis*.

3.4. Lice infestation levels

No sessile lice (copepodids, chalimus I and II stages) were observed on fish prior to December 2019. After back calculating observed counts (February 2020 onwards) of each of the different sessile lice stages to their corresponding mean infection date, there was no interaction between time and cage type (RM time*cage: $F_{GG.24,\ 9.5} = 3.4$, $p = 0.07$), but the occurrence of new lice increased for both cage types over time (RM time: $F_{GG.24,\ 9.5} = 19.5$, $p < 0.001$, Fig. 5a). Furthermore, from January 2020 to June 2020 new lice infestation counts were 55 ± 37% (mean ± SD) lower in submerged cages than control cages (RM cage: $F_{1,4} = 13.9$, $p = 0.02$). The effect of cage type was strongest during late winter (SM cage: 13th Mar 2020, $F_{1,5} = 55$, $p = 0.002$; 18th Mar 2020, $F_{1,5} = 18.3$, $p = 0.01$ Fig. 5a) where there was 93% less new lice on submerged fish than control fish.

Mobile lice (Pre adult I and II stages) were first observed on fish in February 2020. For the pre-adult stage I there was an interaction between cage type and time (RM time*cage: $F_{4,\ 16} = 4.5$, $p = 0.012$, Fig. 5b). As lice numbers increased for both cage types over time, pre-adult I lice counts were 2.2 times more abundant on fish in control cages than submerged cages in late March 2020 (SM cage: 26th Mar 2020, $F_{1,5} = 16.5$, $p = 0.015$). For the pre-adult stage II a similar

interaction between cage type and time occurred (RM cage*time: $F_{4,16} = 3.1$, $p = 0.046$), however simple means test did not detect any specific time points where there was a significant difference between cage types (SM cage type: Feb, Mar, May, Jun: $F_{1,5} = 0.9$ to 4.2, $p > 0.1$ for all, Fig. 5b).

Adult lice numbers prior to December 2019 were negligible (0 to 0.02 per fish). Post December 2019, there was no interaction effect between time and cage type (RM time*cage: Female $F_{4,16} = 2$, $p = 0.14$, Male $F_{4,16} = 2.7$, $p = 0.07$), but a main effect of time showed male and female lice numbers per fish increased from December 2019 to June 2020 (RM time: Female, $F_{4,16} = 18$, $p < 0.001$, Male, $F_{4,16} = 31$, $p < 0.001$ Fig. 5c). While female or male lice numbers did not vary with cage type (RM cage: Female $F_{1,4} = 3.3$, $p = 0.14$, Male $F_{1,4} = 0.9$, $p = 0.4$), in control cages in May 2020, female adult lice counts were 2.7 times higher and males 1.7 times higher, compared to submerged cages.

3.5. Behavioural observations

3.5.1. Surface activity

Surface activity was initially quite variable in the first few weeks after sea cage transfer, but then settled thereafter for the rest of the grow out period (Fig. 6a). There was no interaction between time and cage type over the trial period (RM time*cage: $F_{GG\ 1.9,\ 7.8} = 3.6$, $p = 0.07$), but there were main effects of time (RM time: $F_{GG\ 1.9,\ 7.8} = 9.2$, $p = 0.01$) and cage type (RM cage: $F_{1,4} = 110$, $p < 0.001$). Pairwise comparisons showed there was 3 times more surface activity for all fish in trial week 3 compared to trial week 22 (PC Week 3 > Week 22, $p = 0.03$). Simple means tests for cage type, indicated that in 12 of the last 16 weeks (late February to mid-June 2020) there was more surface activity in control cages than submerged cages (SM Weeks 20, 34, 36, 37, 38, 39, 43, 44, 45, 46,47, 49 and 50, control > submerged: $F_{1,5} = 9$ to 213, $p < 0.05$ for all, Fig. 6a). During this period, the number of surface breaks per fish per hour (No. fish^{-1} h^{-1}) across weeks ranged from 0.02 to 0.32 in control cages and from 0.01 to 0.13 in submerged cages. There was 1 week at the end of October 2019 when surface activity was higher in the submerged cages (SM Trial week 18 submerged > control: $F_{1,5} = 18$, $p = 0.01$, Fig. 6a).

3.5.2. Swim speeds

Swimming speeds for control and submerged fish followed a similar pattern over the trial period and weekly speeds ranged from (mean ± SE) 0.4 ± 0.01 to 1.1 ± 0.11 BL s^{-1} for controls and 0.4 ± 0.03 to 1.2 ± 0.04 BL s^{-1} for submerged (Fig. 6b). There was no interaction between time and cage type (RM time*cage: $F_{GG\ 3.5,\ 14} = 2.65$, $p = 0.08$) or main effect of cage type (RM cage: $F_{1,4} = 0.28$, $p = 0.6$. A main effect of time (RM time: $F_{GG\ 3.5,\ 14} = 14.8$, $p < 0.001$) indicated swim speeds for all fish were faster in some weeks, early in the trial compared to later in the trial. (Pairwise comparisons for time: Trial week 12 > 27, 42, 43, 45, 50; Week 15 > 30; Week 16 > 30, 40, 41, 43, 50; Week 18 > 41, 45, 50; Week 20 > 47, 50, Week 21 & 22 > 50, $p < 0.05$ for all).

3.5.3. Swim depth and relative echo strength

Fish in both control and submerged cages generally swam in the warmest areas of their respective cage types (Fig. 1a). Using mean fish depth as a proxy for estimating weekly fish temperature (Fig. 1a) and oxygen (Fig. 1c) experienced, control fish experienced a total of 3896 degree days and submerged fish 3601 degree days. The majority of extra 295 day-degrees experienced by control fish occurred during summer in 2019. For oxygen, prior to March 2020 control fish experienced (mean ± 1 SD) a weekly oxygen saturation level of 91 ± 11%, and submerged fish 87 ± 9%. Post March 2020 to mid-June 2020, on average control fish experienced 107 ± 10% and submerged 72 ± 11% oxygen saturation. While the relative echo strength was initially highly variable for both submerged and control fish, it followed a similar pattern for both cage types over the 12 months (Fig. 6c) with no obvious deviations at any stage relative to a specific cage type, indicating all fish were able to maintain a similar swim bladder fullness during grow-out.

3.5.4. Surface activity at harvest

When the net ceilings were lifted from submerged cages prior to harvest, the greatest increase in surface activity in submerged fish was observed around 90 min post net ceilings being lifted, but this was not different to activity levels in control cages (RM time*cage: $F_{GG2.8,\ 11} = 2.0$, $p = 0.17$; RM time: $F_{GG2.8,\ 11} = 0.9$ $p = 0.48$; RM cage: $F_{1,4} = 4.3$, $p = 0.11$, Fig. 7). Submerged fish activity ranged from 0 to 0.7 surface breaks fish^{-1} h^{-1} and control fish activity ranged from 0.1 to 0.5 surface breaks fish^{-1} h^{-1}. Accumulated surface activity per cage over the 210 min after full removal of the net ceiling was 3720 ± 317 and 11,085 ± 3943 in control and submerged cages equivalent to 1.9 ± 0.7 and 0.8 ± 0.3 times per fish (mean ± SD respectively). This would equate to estimated totals of 12 and 5.6 times per fish per day (respectively) if the level was upheld.

4. Discussion

This is the first full-production cycle study to grow Atlantic salmon in submerged cages from sea transfer to harvest. The addition of an air-dome to submerged cages enabled salmon to refill their swim bladders and maintain normal swimming behaviour while submerged below 15 m deep for a period of 12 months. While long-term submergence reduced salmon lice infestation rates, production problems arose, as evidenced by the poorer growth, mortality and welfare experienced by submerged fish. These outcomes were tightly linked to the very different production environment that submerged fish experienced at this site compared to the surface cages, with sub-optimal temperatures and dissolved oxygen conditions for extended periods. A key conclusion of the study is that for submergence to be a successful strategy to alleviate problems such as sea lice infestations, submergence must be matched to farming sites and times when conditions at depth are optimal for production.

4.1. Fish growth and welfare

4.1.1. Growth

Differences in growth parameters between control and submerged fish over the grow-out period (SGR by 4 months, weight gain by 6 months, condition factor K by 9 months) resulted in control fish being near double the weight of submerged fish at harvest. In a previous short-term submergence trial (<2 months) with air domes fitted to cages, no effect on growth was apparent (Oppedal et al., 2020). Without an air-dome, reports on growth during short term submergence (<1 month)

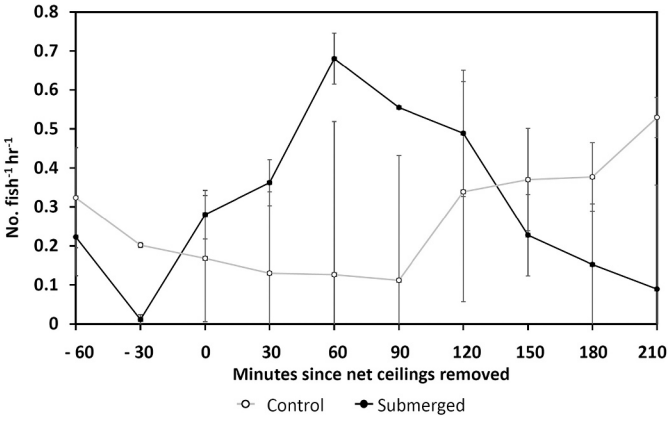

Fig. 7. Surface activity of Atlantic salmon in submerged cages and surface access (control) cages, in the first 3½ hrs post net ceiling removal. Each time point represents number of surface breaks fish^{-1} h $^{-1}$ ±− SE from 3 control cages (open circles) and 3 submerged cages (closed circles).

have varied from no effect (Dempster et al., 2009) to poorer growth and welfare (Dempster et al., 2008; Korsøen et al., 2009). Negative effects on growth can be alleviated, if submerged fish are given once weekly access to the surface to refill their swim bladders (Glaropoulos et al., 2019). However, it would be impractical for commercial farms to have to raise and lower submerged cages weekly. There are no previous reports of long-term submergence of Atlantic salmon with or without the use of an airdome to determine if the effects of submergence on growth in this study were farm site specific or not. However, within the site, there were stark differences in environmental conditions between control and submergence cages during grow-out that are indicative of the causes behind why poorer growth in submerged fish occurred.

Temperature and oxygen levels experienced by fish varied during certain periods of the trial (Fig. 1). Overall, control fish experienced approximately 295 extra degree days than submerged fish, meaning it is plausible that control fish had more optimal temperatures for growth (e.g. Sambraus et al., 2018), particularly early on, when the temperature difference was highest. This would explain the steeper weight gain trajectory of control fish compared to submerged fish (Fig. 2a). Differences in degree days experienced by salmon during a short-term submergence trial (<3 weeks) has been previously reported to be the cause of reduced growth rates in submerged fish (e.g. Dempster et al., 2008). Oxygen saturation levels were similar between cage types for most of the trial up until March 2020, whereafter submerged fish experienced a sub-optimal oxygen environment which would have exacerbated their poorer growth rate (Remen et al., 2013, 2016) and may also explain the increase in mortality rate that started around this time. Feed intake is reduced when dissolved oxygen levels drop below 55% saturation in 11 °C waters (Remen et al., 2016). Furthermore, within cages, oxygen saturation levels are on average 35% less compared to reference measurements outside (Johansson et al., 2007; Solstorm et al., 2018; Oldham et al., 2018) and can vary by up to 35% among cages within a farm (Burke et al., 2021) meaning that dissolved oxygen values in submerged cages were likely below the 55% thresholds for reduced appetite for periods during the last few months of the trial.

The feed deliver system is another potential issue in this trial that may have contributed to poorer growth in submerged fish as submerged fish received feed from a single point source via a pipe, making the feed dispersion area much smaller compare to control cages. This would have resulted in feeding aggregations being denser, with more competition for feed in submerged cages, causing more injures and increasing the likelihood of disease. While excess feed accumulating at the bottom of the cage was used as a visual indicator of feeding to satiation, it is possible due to the feed delivery system, submerged fish were less efficient at feeding, resulting in fish being fed less. Future submergence trials should test feed distribution systems that can provide a dispersed feed area and use an appropriate method to accurately estimate total feed consumption (e.g., Dempster et al. (2009)) to see if better feeding will alleviate both growth and welfare problems.

4.1.2. SWIM scores

There was minimal change in fin and skin condition SWIM scores over the grow out period, indicating the addition of the dome structure and net ceiling has little effect on salmon fin and skin condition. This is a good positive result in terms of fish welfare for fish held in submerged cages. However, higher incidence of mouth jaw wounds is of concern. No observations of mouth jaw wounds were reported in a previous 7-week submergence trial using an airdome (Oppedal et al., 2020) which aligns with what was observed in the first few months of this trial. Yet, while some increase in the occurrence of mouth jaw wounds as fish grow may be expected (occurred in both control and submerged fish) the significantly higher final SWIM scores for submerged fish (2.7 SWIM points vs 1.5 in controls) suggest either the airdome, or the net ceiling may be exacerbating the level of injury to the mouth and snout area of fish in submerged cages. Signs of *Tenacibaculum* sp. observed on a high proportion of the dead fish from submerged cages can cause mouth injuries (Avendaño-Herrera et al., 2006). As lower salinity may alleviate the effects and occurrence for *Tenacibaculum* (Soltani and Burke, 1994), some of the difference observed in the severity of mouth jaw wounds between cage types may be due to control fish having access to brackish surface waters, particularly in spring when their snout index decreased whilst submerged fish continuously occupied full strength salinity. Deteriorating eye condition and mouth jaw wounds in submerged fish began to occur after the feeding method was change and oxygen levels started to drop. Although not observed, this may have caused a change in fish behaviour creating increased competition for food or attempts to move to better environmental conditions (more oxygen), possibly causing increased scraping against the net ceiling. As major mouth injuries can inhibit farmed salmon's ability to feed (Noble et al., 2012) this may also be one of the contributing factors to the slower growth observed in submerged fish relative to control fish, in winter and spring. There was also a gradual deterioration in eye condition over the grow out period, and more so in submerged fish and control fish, particularly closer to the end of the trial. However, while mean eye condition SWIM scores for submerged fish were near twice that of control fish indicating submergence did have some effect on general eye health, eye condition scores around 2 or less are still within the acceptable level with regards to SWIM welfare scores for salmon in commercial cages (Stien et al., 2013).

4.1.3. Lice levels

Creating a spatial barrier between salmon lice in the upper surface waters and salmon submerged at depth is a pro-active way to reduce the encounter rate between salmon and the infective copepodite stage of salmon lice. Minimal lice were observed on fish prior to December 2019. Subsequently, thereafter infestation increased, and the first major lice pulse saw a 93% lower infestation level for submerged fish compared to control fish. This is comparable to Sievers et al. (2018) reported 72% reduction in infective lice on fish submerged 10 m below the surface and average reduction of 75% in 10 m snorkel cages (Geitung et al., 2019). The substantial impact in reducing the initial infection numbers from a large pulse, resulted in a measurable reduction in the numbers of the next lice development stage (pre-adult stage 1) in late March 2020. Whilst thereafter the effect was no longer significantly detectable, the remnants of a lower infestation period in submerged cages in March appears to have had some follow on effect into the adult stages as adult male and female lice counts were still 1.7 and 2.7 times higher in control cages in May (Fig. 5c) by which time any new lice that infected fish in March would have reached the final adult stage. There may be several reasons why limiting the infection rate, did not translate into statistically lower pre-adult II and adult lice numbers on submerged fish after March 2020. From December 2019, submerged fish were generally worse in terms of growth and key SWIM welfare metrics, indicating their overall immune health was potentially poorer. Hence, while submerged fish may have experienced a lower relative infection rate during the winter, it is possible that the survival rate of infective lice on submerged fish was higher. In many primary production systems, once animals have a compromised immune system, they can have less resistance to disease or parasites once infected (Colditz, 2002; Fast, 2014). It is also plausible that despite the higher initial infestation rate in control fish in March 2020, their freedom of access to lower salinity surface waters (Fig. 1) may have enabling control fish to shed some lice (Bricknell et al., 2006; Jones and Hargreaves, 2007) somewhat reducing their effective adult lice numbers relative to submerged fish. A third plausible reason is the addition of cleaner fish (Lumpfish, *C. lumpus*) to all cages in February 2020 at the farm site to help control lice numbers, may have resulted in more effective adult lice removal from fish in control cages than submerged cages, as previous research has indicated the efficacy of cleaner fish is influenced by the cage environment they are held in (Gentry et al., 2020). As an example, lumpfish have been shown to have an efficiency of reducing adult lice levels of 53–73% (Imsland et al., 2018), yet analysis of commercial data indicated variable to no effect (Barrett et al.,

2020b).The cold water species lumpfish may also be more efficient if they resided in the more preferred cold surface waters in control cages (observed from March to May 2020, Fig. 1) compared to the slightly warmer water temperature deep down (Geitung et al., 2020) in submerged cages during the same period. Echosounder data indicated that the average salmon in both the control and submerged cages generally resided in 10–11 degree C water during this time, but it was not known as to where the average lumpfish resided in the cage during this period.

4.2. Behavioural observations

4.2.1. Swim bladder fullness

Based on relative echo strength observations no apparent decreases in the swim bladder fullness were observed in any period. This matches Oppedal et al. (2020) and is not like what is seen when salmon are submerged without air access (Dempster et al., 2009; Korsøen et al., 2009; Sievers et al., 2018; Glaropoulos et al., 2019). Hence in this study it may be concluded the underwater airdome acted as a suitable alternative source of air for submerged fish to maintain appropriate swim bladder fullness.

4.2.2. Surfacing behaviour and swim speeds

Salmon surfacing behaviour was similar between cage types during the first 8 months, but more surface activity in terms of jumps and rolls was observed in control cages (0.25 to 1.1 fish^{-1} h^{-1}) than submerged cages (0.08 to 0.27 fish^{-1} h^{-1}) from March 2020 onwards. Yet, there was no observations of tail-down-head-up swimming behaviour, or increased swimming speeds in submerged cages which is typical of salmon with underinflated swim bladders (Korsøen et al., 2009; Sievers et al., 2018). This indicates fish in submerged cages were able to maintain their balance, despite showing marginally less surfacing behaviour towards the end of the trial. While both measures of surface activity may be considered within the range of normal expected activity levels (Dempster et al., 2009; Oppedal et al., 2020). Lower levels of activity in submerged fish later in the trial may be attributed to their increase in size and lipid levels. As the fish grow, a larger, fatter fish will have a deeper maximum neutral buoyancy depth (Macaulay et al., 2020) and the need for refilling is reduced. Furthermore, salmon refilling air at 15 m deep with an air pressure of 2.5 bar and swimming depth range of 15–30 m (2.5–4 bar) may be more efficient than for a salmon refilling at the surface (1 bar) with a swimming depth range of 0–15 m (1–2.5 bar). Hence, the relative change in air pressure and swim bladder volume between submerged and control fish may indicate control fish have a higher need for refilling compared to submerged fish. The lack of lowered activity of submerged fish relative to control fish later in the trial could also be plausibly explained by increased activity from higher levels of lice, as seen by Furevik et al. (1993). Leaping activity can increase with lice level, but this was only rarely observed in submerged fish possibly due to both a somewhat lower lice level, and the restriction in surface access inside the dome area.

Submergence had no influence on swim speeds during the sea cage production period. Initial swim speeds ranged from 0.4 to 1.2 BL *sec*$^{-1}$, displaying a gradual decrease as the trial progressed to stabilised between 0.3 and 0.7 BL sec^{-1} which is expected as fish increase in size (e.g. Oldham et al., 2019). Previous reported swim speeds for 0.5 to 1.5 kg fish submerged for 7 weeks, ranged from 0.6 to 1.1 BL sec^{-1} (Oppedal et al., 2020) is comparable to swim speeds observed in the early months of this study when fish were of a similar size. The typical range of normal swimming speeds for Atlantic salmon grown in open surface access sea cages has been reported to be from 0.2 to 1.9 BL sec $^{-1}$ (e.g. Oppedal et al., 2011; Hansen et al., 2017) which also overlaps with what was observed in this trial.

4.2.3. Surface behaviour prior to harvest

Once the net ceilings were removed, there was a gradual increase in surface behaviour in terms of jumps and rolls in the submerged cages that peaked at 0.8 surface roll fish^{-1} h^{-1}, 90 min post removal, but this was not statistically different to surface activity in control fish. The marginal increase in surfacing behaviour and the time in that this occurred in was not typical of what would be expected of salmon if they had empty swim bladders. Dempster et al. (2008) and Glaropoulos et al. (2019) reported bursts of intensive surface behaviour, 10–50 times above normal, in the first 30 min after surface access was restored to salmon submerged for 2, 4 or 7 days without an airdome. Lifting the submerged cages may result in the salmon partially emptying their swim bladders to compensate for the ascent to shallower waters, and both feeding and stress reaction can also lead to increase swim bladder emptying (e.g. Nøttestad, 1998; Bui et al., 2013a, 2013b). A salmon's ability to accurately control the rate that it can empty its swim bladder to adjust buoyancy, as with refilling (Macauley et al., 2020), is unknown. Hence, there are potentially multiple indicators that the minor increase in surface activity may be a consequence of a need for the salmon to slightly readjust their buoyancy after resurfacing.

4.3. Submergence

The success of submerged cage culture depends on the suitability of the species being cultured, and the ambient environmental conditions fish experience at depth which may vary considerably among farm locations, or time of year. Here, a main aim of submerging Atlantic salmon at depth was to create a spatial mismatch between salmon and salmon lice to reduce lice infestation rates during the sea cage phase of production. Salmon need access to air to maintain neutral buoyancy and normal swimming behaviour, which was successfully accommodated for by the addition of an airdome to each submerged cage. However, while submergence was successful in terms of reducing infestation during a large infestation period, the consequences of keeping fish submerged for the entire production cycle was more detrimental to overall production, as it resulted in submerged fish being cultured for periods in sub optimal environmental conditions (lower temperature and oxygen levels) relative to the environment control fish were cultured in. The occurrence of lower oxygen at depth here contradicts Solstorm et al. (2018) study on commercial salmon cages in the Fensfjorden that reported the lowest oxygen levels occurred in surface waters. Hence, a lower oxygen environment at depth may not be the case for all fjords, or if cages are further offshore, in oceanic waters. Ensuring salmon experience their preferred environmental conditions is central to achieving optimal growth in sea cages (Oppedal et al., 2011) and both temperature (Johansson et al., 2006) and oxygen levels (Solstrom et al., 2018; Remen et al., 2016) play an important role. Atlantic salmon optimal temperatures for growth are around 15 (9–18) °C° for small (Sambraus et al., 2017) and 12 (9–15) °C (Sambraus et al., 2018) for larger salmon, yet here, while submerged fish were often within this range for the majority of the trial, overall they effectively experience 295 degree days less than control fish, meaning control fish experienced more optimal growing conditions. Optimal oxygen levels are critical for maintaining feeding activity (Oppedal et al., 2011; Remen et al., 2013, 2016) and submerged fish also experience an extended period with low dissolved oxygen, which would have compounded the effects of lower temperatures with regards to weight gain for submerged fish in the latter period. The combination of these two environmental factors may be accountable for the main differences in fish growth. Future submergence trials should focus on dynamic use of submerged cages to ensure fish are positioned in an optimal environment over the entire production cycle whilst also enabling an avoidance method for reducing the encounter rate between salmon and salmon lice during periods when high lice numbers are predicted to be present in the marine environment.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2021.737570.

References

Avendaño-Herrera, R., Toranzo, A.E., Magariños, B., 2006. *Tenacibaculosis* infection in marine fish caused by *Tenacibaculum maritimum*: a review. Dis. Aquat. Org. 71, 255–266.

Barrett, L.T., Oppedal, F., Robinson, N., Dempster, T., 2020a. Prevention not cure: a review of methods to avoid sea lice infestations in salmon aquaculture. Rev. Aquacult. 1-17.

Barrett, L.T., Overton, K., Stien, L.H., Oppedal, F., Dempster, T., 2020b. Effect of cleaner fish on sea lice in Norwegian salmon aquaculture: a national scale data analysis. Int. J. Parasitol. 50, 787–796.

Benetti, D.D., O'Hanlon, B., Rivera, J.A., Welch, A.W., Maxey, C., Orhun, M.R., 2010. Growth rates of cobia (*Rachycentron canadum*) cultured in open ocean submerged cages in the Caribbean. Aquaculture 302, 195–201.

Bjordal, Å., Juell, J.E., Lindem, T., Fernö, A., 1993. Hydroacoustic monitoring and feeding control in cage rearing of Atlantic salmon (*Salmo salar L.*). In: Reinertsen, H., Dahle, L.A., Jørgensen, L., Tvinnereim, K. (Eds.), Fish Farming Technology. Balkema, Rotterdam, pp. 203–208.

Bricknell, I.R., Dalesman, S.J., O'Shea, B., Pert, C.C., Luntz, A.J.M., 2006. Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. Dis. Aquat. Org. 71, 201–212.

Bui, S., Oppedal, F., Korsøen, Ø.J., Dempster, T., 2013a. Modifying Atlantic salmon behaviour with light or feed stimuli may improve parasite control techniques. Aquacult. Environ. Interact. 3, 125–133.

Bui, S., Oppedal, F., Korsøen, Ø.J., Sonny, D., Dempster, T., 2013b. Group behavioural responses of Atlantic salmon (*Salmo salar L.*) to light, infrasound and sound stimuli. PloS One 8, e63696.

Bui, S., Stien, L.H., Nilsson, J., Trengereid, H., Oppedal, F., 2020. Efficiency and welfare impact of long-term simultaneous in situ management strategies for salmon louse reduction in commercial sea cages. Aquaculture 520, 734934.

Burke, M., Grant, J., Filgueira, R., Stone, T., 2021. Oceanographic processes control dissolved oxygen variability at a commercial Atlantic salmon farm: application of a real-time sensor network. Aquaculture 533, 736143.

Chambers, M.D., Howell, W.H., 2006. Preliminary information on cod and haddock production in submerged cages off the coast of New Hampshire, USA. ICES J. Mar. Sci. 63, 385–392.

Colditz, I.G., 2002. Effects of the immune system on metabolism: implications for production and disease resistance in livestock. Livest. Prod. Sci. 75, 257–268.

Costelloe, J., Costelloe, M., Roche, N., 1995. Variation in sea lice infestation on Atlantic salmon smolts in Killary harbour, west coast of Ireland. Aquacult. Int. 3, 379–393.

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*) in sea-cages: a potential short-term solution to poor surface conditions. Aquaculture 288, 254–263.

Fast, M.D., 2014. Fish immune responses to parasitic copepod (namely sea lice) infection. Dev. Comp. Immunol. 43, 300–312.

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.

Geitung, L., Oppedal, F., Stien, L.H., Dempster, T., Karlsbakk, E., Nola, V., Wright, D.W., 2019. Snorkel Sea-cage technology decreases salmon louse infestation by 75% in a full-cycle commercial test. Int. J. Parasitol. 49, 843–846.

Geitung, L., Wright, D.W., Oppedal, F., Stien, L.H., Vågseth, T., Madaro, A., 2020. Cleaner fish growth, welfare and survival in Atlantic salmon sea cages during an autumn-winter production. Aquaculture 528, 735623.

Gentry, K., Bui, S., Oppedal, F., Dempster, T., 2020. Sea lice prevention strategies affect cleaner fish delousing efficacy in commercial Atlantic salmon sea cages. Aquacult. Environ. Interact. 12, 67–80.

Glaropoulos, A., Stien, L.H., Folkedal, O., Dempster, T., Oppedal, F., 2019. Welfare, behaviour and feasibility of farming Atlantic salmon in submerged cages with weekly surface access to refill their swim bladders. Aquaculture 502, 332–337.

Grøntvedt, R.N., Kristoffersen, A.B., Jansen, P.A., 2018. Reduced exposure of farmed salmon to salmon louse (*Lepeophtheirus salmonis* L.) infestation by use of plankton nets: estimating the shielding effect. Aquaculture 495, 865–872.

Hamre, L.A., Bui, S., Oppedal, F., Skern-Mauritzen, R., Dalvin, S., 2019. Development of the salmon louse *Lepeophtheirus salmonis* parasitic stages in temperatures ranging from 3 to 24 °C. Aquaculture Environment Interactions 11, 429–443.

Hansen, T.J., Fjelldal, P.G., Folkedal, O., Vågseth, T., Oppedal, F., 2017. Effects of light source and intensity on sexual maturation, growth and swimming behaviour of Atlantic salmon in sea cages. Aquacult. Environ. Interact. 9, 193–204.

Hvas, M., Folkedal, O., Imsland, A., Oppedal, F., 2017. The effect of thermal acclimation on aerobic scope and critical swimming speed in Atlantic salmon, *Salmo salar*. J. Exp. Biol. 220, 2757–2764.

Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Foss, A., Vikingstad, E., Elvegård, T.A., 2014. The use of lumpfish (*Cyclopterus lumpus* L.) to control sea lice (*Lepeophtheirus salmonis* Krøyer) infestations in intensively farmed Atlantic salmon (*Salmo salar* L.). Aquaculture 424, 18–23.

Imsland, A.K.D., Hanssen, A., Nytrø, A.V., Reynolds, P., Jonassen, T.M., Hangstad, T.A., Elvegård, T.A., Urskog, T.C., Mikalsen, B., 2018. It works! Lumpfish can significantly lower sea lice infestation in large-scale salmon farming. Biol Open. 7 (9).

Johannessen, A., 1978. Early stages of *Lepeophtheirus salmonis* (Copepoda: Caligidae). Sarsia 63, 169–176.

Johansson, D., Ruohonen, K., Kiessling, A., Oppedal, F., Stiansen, J.-E., Kelly, M., Juell, J.-E., 2006. Effect of environmental factors on swimming depth preferences of Atlantic salmon (*Salmo salar L.*) and temporal and spatial variations in oxygen levels in sea cages at a fjord site. Aquaculture 254, 594–605.

Johansson, D., Juell, J.E., Oppedal, F., Stiansen, J.E., Ruohonen, K., 2007. The influence of the pycnocline and cage resistance on current flow, oxygen flux and swimming behaviour of Atlantic salmon (*Salmo salar* L.) in production cages. Aquaculture 265, 271–287.

Jones, S.R.M., Hargreaves, N.B., 2007. The abundance and distribution of *Lepeophtheirus salmonis* (Copepoda: caligidae) on pink (*Oncorhynchus gorbuscha*) and chum (*O. Kita*) salmon in coastal British Columbia. J. Parasitol. 93, 1324–1331.

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.

Macaulay, G., Wright, D., Oppedal, F., Dempster, T., 2020. Buoyancy matters: establishing the maximum neutral buoyancy depth of Atlantic salmon. Aquaculture 519, 734925.

Maricchiolo, G., Mirto, S., Caruso, G., Caruso, T., Bonaventura, R., Celi, M., Matranga, V., Genovese, L., 2011. Welfare status of cage farmed European sea bass (*Dicentrarchus labrax*): a comparison between submerged and surface cages. Aquaculture 314, 173–181.

McKibben, M.A., Hay, D.W., 2004. Distributions of planktonic sea lice larvae *Lepeophtheirus salmonis* in the inter-tidal zone in loch Torridon, Western Scotland in relation to salmon farm production cycles. Aquac. Res. 35, 742–750.

Noble, C., Jones, H.A.C., Damsgård, B., Flood, M.J., Midling, K.Ø., Roque, A., Sæther, B. S., Cottee, S.Y., 2012. Injuries and deformities in fish: their potential impacts upon aquacultural production and welfare. Fish Physiol. Biochem. 38, 61–83.

Norwegian Ministry of Trade and Fisheries, 2012. Regulations on Combating Salmon Lice in Aquaculture Farms (in Norwegian: Forskrift om bekjempelse av lakselus i akvakulturanlegg). Norway. Lovdata.no.

Nøttestad, L., 1998. Extensive gas bubble release in Norwegian spring-spawning herring (*Clupea harengus*) during predator avoidance. ICES J. Mar. Sci. 55, 1133–1140.

Oldham, T., Oppedal, F., Dempster, T., 2018. Cage size affects dissolved oxygen distribution in salmon aquaculture. Aquacult. Environ. Interact. 10, 149–156.

Oldham, T., Nowak, B., Hvas, M., Oppedal, F., 2019. Metabolic and functional impacts of hypoxia vary with size in Atlantic salmon. Comp. Biochem. A 231, 30–38.

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., Samsing, F., Dempster, T., Wright, D.W., Bui, S., Stien, L.H., 2017. Sea lice infestation levels decrease with deeper 'snorkel' barriers in Atlantic salmon sea-cages. Pest Manag. Sci. 73, 1935–1943.

Oppedal, F., Bui, S., Stien, L.H., Overton, K., Dempster, T., 2019. Snorkel technology to reduce sea lice infestations: efficacy depends on salinity at the farm site, but snorkels have minimal effects on salmon production and welfare. Aquacult. Environ. Interact. 11, 445–457.

Oppedal, F., Folkedal, O., Stien, L.H., Vågseth, T., Fosse, J.O., Dempster, T., Warren-Myers, F., 2020. Atlantic salmon cope in submerged cages when given access to an air dome that enables fish to maintain neutral buoyancy. Aquaculture 525, 1–7.

Remen, M., Oppedal, F., Torgersen, T., Imsland, A.K., Olsen, R.E., 2013. Effects of cyclic environmental hypoxia on physiology and feed intake of post-smolt Atlantic salmon: initial responses and acclimation. Aquaculture 326, 148–155.

Remen, M., Sievers, M., Torgersen, T., Oppedal, F., 2016. The oxygen threshold for maximal feed intake of Atlantic salmon post-smolts is highly temperature dependent. Aquaculture 464, 582–592.

Sambraus, F., Olsen, R.E., Remen, M., Hansen, T.J., Torgersen, T., Fjelldal, P.G., 2017. Water temperature and oxygen: the effect of triploidy on performance and metabolism in farmed Atlantic salmon (*Salmo salar* L.) post-smolts. Aquaculture 473, 1–12.

Sambraus, F., Remen, M., Olsen, R.E., Hansen, T.J., Waagbø, R., Torgersen, T., Lock, E.J., Imsland, A., Fraser, T.W., Fjelldal, P.G., 2018. Changes in water temperature and oxygen: the effect of triploidy on performance and metabolism in large farmed Atlantic salmon. Aquacult. Environ. Interact. 10, 157–172.

Sievers, M., Korsøen, Ø., Dempster, T., Fjelldal, T., Kristiansen, T., Folkedal, O., Oppedal, F., 2018. Growth and welfare of submerged Atlantic salmon under continuous lighting. Aquacult. Environ. Interact. 10, 501–510.
Solstorm, D., Oldham, T., Solstorm, F., Klebert, P., Stien, L.H., Vågseth, T., Oppedal, F., 2018. Dissolved oxygen variability in a commercial sea-cage exposes farmed Atlantic salmon to growth limiting conditions. Aquaculture 486, 122–129.
Soltani, M., Burke, C.M., 1994. Responses of fish-pathogenic Cytophaga/Flexibacter-like bacteria (CFLB) to environmental conditions. Bull. Eur. Assoc. Fish Pathol. 4, 185–187.
Stien, L.H., Bracke, M.B., Folkedal, O., Nilsson, J., Oppedal, F., Torgersen, T., 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. Aquacult. 5, 33–57.
Stien, L.H., Dempster, T., Bui, S., Glaropoulos, A., Fosseidengen, J.E., Wright, D.W., Oppedal, F., 2016. 'Snorkel' sea lice barrier technology reduces sea lice loads on harvest-sized Atlantic salmon with minimal welfare impacts. Aquaculture 458, 29–37.
Stien, L.H., Lind, M.B., Oppedal, F., Wright, D.W., Seternes, T., 2018. Skirts on salmon production cages reduced salmon lice infestations without affecting fish welfare. Aquaculture 490, 281–287.
Wade, N.M., Clark, T.D., Maynard, B.T., Atherton, S., Wilkinson, R.J., Smullen, R.P., Taylor, R.S., 2019. Effects of an unprecedented summer heatwave on the growth performance, flesh colour and plasma biochemistry of marine cage-farmed Atlantic salmon (*Salmo salar*). J. Therm. Biol. 80, 64–74.
Wright, D.W., Stien, L.H., Dempster, T., Vågseth, T., Nola, V., Oppedal, F., 2017. 'Snorkel' lice barrier technology reduced two co-occurring parasites, the salmon louse (*Lepeophtheirus salmonis*) and the amoebic gill disease causing agent (*Neoparamoeba perurans*), in commercial salmon sea-cages. Prev. Vet. Med. 140, 97–105.
Wright, D.W., Geitung, L., Karlsbakk, E., Stien, L.H., Dempster, T., Oldham, T., Nola, V., Oppedal, F., 2018. Surface environment modification in Atlantic salmon sea-cages: effects on amoebic gill disease, salmon lice, growth and welfare. Aquacult. Environ. Interact. 10, 255–265.