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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

Frode Oppedal[1], Samantha Bui[1], Lars H. Stien[1], Kathy Overton[2], Tim Dempster[2,*]

[1]Institute of Marine Research, 5984 Matredal, Norway
[2]Sustainable Aquaculture Laboratory – Temperate and Tropical (SALTT), School of Biosciences, University of Melbourne, 3010 Victoria, Australia

ABSTRACT: Sea lice are a critical health issue in most salmonid farming regions. New cage-based technologies can prevent infestations from occurring, such as the 'snorkel', which introduces an impermeable barrier that separates salmon lice *Lepeophtheirus salmonis* from Atlantic salmon *Salmo salar* in the surface waters where lice are most abundant. While snorkels provide protection from lice, their lice-reducing effect can vary under different environmental conditions. We conducted production-scale sea-cage experiments at 2 sites with contrasting salinity environments in Norway. At the coastal site, with a weak and unsystematic halocline, snorkels reduced lice infestations by 76%. However, at the fjord site, with brackish surface waters and a strong halocline, snorkels did not reduce lice relative to control cages, likely because both lice and salmon remained deeper in the water column below the brackish layer, and infection rate was similar. At the fjord site, as lice numbers between snorkel and control cages were similar, we tested for differences in the absence of the potentially confounding effect of different lice levels. Snorkel cages at the fjord site modified swimming speeds (1.14 times faster), surface breaching behaviours (2.8 times less), and total echo-sounder signal strength of fish (an index of swim bladder fullness; 30–40% less) relative to control cages. Production parameters remained similar, but snout condition was poorer in snorkel cages, suggesting more frequent contact with cage netting. Our results suggest that salinity is a significant environmental factor that alters the lice-reducing efficacy of depth-based technologies such as snorkels. Further, snorkels affect salmon behaviour, which must be considered in welfare assessments of their use.

KEY WORDS: Atlantic salmon · Behaviour · *Salmo salar* · Salmon lice · Swimming activity · *Lepeophtheirus salmonis* · Aquaculture

1. INTRODUCTION

Sea lice (*Lepeophtheirus salmonis* and *Caligus* spp.) outbreaks are often dealt with through prophylactic, chemotherapeutant-infused feeds (Stone et al. 1999), topical bathing treatments (Roth et al. 1993), biological control (e.g. cleaner fish; Groner et al. 2013), or through mechanical and thermal delousing (Overton et al. 2018) once infestations have occurred. Thermal treatments are currently the most commonly used delousing operation administered in Norwegian salmon aquaculture (>61% registered thermal treatments in 2017; Overton et al. 2018). Thermal, mechanical, and chemotherapeutant treatments can lead to poor post-treatment outcomes for Atlantic salmon (*Salmo salar*; Overton et al. 2018). Further, widespread re-

*Corresponding author: dempster@unimelb.edu.au

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sistance and reduced treatment efficacy for most available chemotherapeutants is spreading across Norway (Aaen et al. 2015). Thus, there is an increasing focus on developing prevention methods that can bypass issues associated with mechanical or chemotherapeutant control methods.

Knowledge of the behaviour of both sea lice and salmon provides the potential for new approaches that seek to spatially de-couple hosts from parasites and prevent infestations from occurring. The infective copepodid stage of the salmon louse *L. salmonis* is pelagic (Johnson & Albright 1991), strongly phototactic (Bron et al. 1993), and actively avoids low-salinity waters (Heuch 1995, Crosbie et al. 2019). These behaviours typically result in greatest abundances at shallow depths, particularly directly beneath haloclines of 30 ppt in coastal waters (Johannessen 1978, Costelloe et al. 1995, 1998, Heuch et al. 1995, McKibben & Hay 2004, Costello 2006). Farmed salmon presumably encounter salmon lice larvae and are therefore most exposed to infestation when they swim in surface waters. Salmon often swim at shallow depths when light and temperature levels are optimal and during feeding periods, as all current commercial feed systems deliver feed to the surface (Oppedal et al. 2011). Moreover, salmon make multiple daily visits to the surface to re-fill their swim bladders to maintain neutral buoyancy (Dempster et al. 2008, 2009, Korsøen et al. 2012).

Depth-based preventative methods harness the spatial and temporal behaviours of salmon and lice to create a mismatch in the environments that the host and parasite occupy. Barrier technologies, such as skirts and snorkel cages, introduce an impermeable lice barrier that allow salmon to swim up from the cage below and refill their swim bladders while simultaneously preventing lice copepodids in the surface layers from entering the cage (Stien et al. 2016, 2018, Oppedal et al. 2017, Wright et al. 2017). As salmon prefer to swim deeper, below the level of the snorkel or skirt, this reduces encounters with copepodids, thereby lowering infestation pressure. Submerged cages are another depth-based preventative technology that is gaining popularity (Dempster et al. 2008, 2009), with promising evidence for reducing lice levels (Hevrøy et al. 2003, Sievers et al. 2018, Glaropoulos et al. 2019).

In previous experiments, we introduced the snorkel into standard sea-cages to minimise encounter rates between salmon lice and salmon and thus reduce infestation levels (Stien et al. 2016, Oppedal et al. 2017, Wright et al. 2017). In many respects, the snorkel cage system creates a cage environment that lies between standard surface production cages and submerged cages (Dempster et al. 2008). Submerging salmon in full-scale sea-cages with no access to the surface for days to months leads to decreased swim bladder fullness, as salmon have no capacity to roll, swallow air from the surface, and refill them (Dempster et al. 2009, Korsøen et al. 2009). This in turn increases swimming speeds by 1.5–1.6 times, and if submergence extends for weeks to months, it can reduce feeding behaviour, growth, and condition. In contrast to fully submerged systems, the snorkel cage structure decouples host from parasite, whilst allowing salmon to access the surface waters to refill their swim bladders. Therefore, effects on growth and condition should lie somewhere between those observed in typical surface-based and submerged cages.

In previous work, Stien et al. (2016) found that salmon held in cages with snorkels installed down to 4 m depth had 24–65% less lice compared to control cages, depending upon the production period. Little or no adverse effects on fish mortality and welfare were detected. Oppedal et al. (2017) tested how varying snorkel depths affected lice infestation levels, and found that as snorkel depth increased (0, 4, 8, 12, and 16 m), lice infestations decreased exponentially. Growth, condition, mortality, swimming speeds, and key welfare indices were similar for all snorkel depths (Oppedal et al. 2017). Wright et al. (2017) found that 10 m deep snorkels in commercial-scale cages reduced new lice infestations by 84%. These previous experiments illustrate varying reductions in lice infestations; however, the experiments were all conducted at locations with relatively unstratified salinity profiles, and there has been no previous research on the effectiveness of snorkel cages in preventing salmon lice infestations at farm sites where brackish layers are persistent.

Understanding the co-evolutionary drivers of host–parasite systems may provide opportunities to reduce encounters and thus prevent infestations using targeted technologies. Based on knowledge of the behaviours of the salmon louse and Atlantic salmon, we hypothesised that the upper water column in salmon farms is the most infestation-risky environment at coastal farming sites with a well-mixed surface layer, which is where most salmon farming now occurs. We tested the hypothesis that introducing lice barriers (snorkels) into the surface waters of salmon cages would reduce infestation levels on salmon by lowering encounter rates with infectious salmon lice copepodids relative to standard farming cages with no barriers. Further, we conducted an additional ex-

periment in a stratified environment with a deeper halocline, where we predicted that the lice barriers would not create a spatial mismatch between hosts and parasites, and since lice would be dispersed deeper to avoid the halocline, no difference in louse infestation levels on salmon would occur. As a result, any differences in production, behaviour, and welfare parameters could then be interpreted as being due to the lice barrier, rather than the potentially confounding effect of different lice levels on fish.

2. MATERIALS AND METHODS

2.1. Lice barrier experiments

2.1.1. Expt 1: Coastal site with unsystematic halocline

The first experiment was conducted from June–August 2012 at a sheltered ocean site at Austevoll, Norway (60.0° N, 5.3° E), where stratification of the water column is typically weak and unsystematic. Under these conditions, the infectious stages of lice would be expected to occur in the upper few metres due to their positive phototaxis (Heuch et al. 1995). Three production-scale sea-cages (12 × 12 × 12 m deep; approx. 1600 m^3) acted as controls, with no manipulation of the cage structure, while 3 sea-cages contained a snorkel, which consisted of a large cylindrical fibreglass tube (diameter: 3 m; height: 4 m) that was open at the top and bottom and attached to a net roof sewn into the sea-cage (see Fig. A1A,B in the Appendix). Floats were attached to the tube 1 m from the top, so that 1 m of the tube was above the water and 3 m was submerged. The net roof was connected to the rim of the tube at the base and sewn into the sea-cage at 4 m depth. Salmon in the lice barrier cages could only access the surface within the tube, where salmon lice were excluded as they could not flow into the area through the solid tube wall, while salmon in control sea-cages could access the entire sea-cage surface. To ensure adequate oxygen concentrations within the tube, a pump was suspended below the base of the tube at 4.5 m and transferred water (110 l min^{-1}) from this depth to the surface inside the tube. The lice barriers were maintained for 76 d.

Sea-cages were stocked with 3000 Atlantic salmon (Aquagen strain; mean ± SE weight: 89.0 ± 2.3 g) in early May. Automated feeders (Betten Maskinstasjon; www.betten-m.no) distributed feed from the surface in control sea-cages and at the surface through the net roof in lice barrier sea-cages. Fish were fed to satiation (waste feed present at the end of the day assessed 5 d wk^{-1} by cameras operated by farm personnel) during continuous feeding over 7 h using a pellet size recommended for fish size (Skretting). Feed supply was adapted according to observed appetite levels.

2.1.2. Expt 2: Fjord site with a strong halocline

The second experiment was conducted from February–April 2013 at the Cage Environment Laboratory at the Institute of Marine Research field station at Matredal in Masfjorden, Norway (60.8° N, 5.4° E). As an inner fjord site, the water column is typically stratified, with a low-salinity layer at the surface due to freshwater inflows from nearby rivers. Under these conditions, the infectious stages of lice would be expected to occur beneath the halocline where salinities first exceeded 30 ppt due to a combination of their avoidance of low-salinity waters and positive phototaxis. The same cage types and lice barriers were used as in Expt 1, with 3 control and 3 snorkel replicates interspersed to remove any possibility of treatment confounding effects due to spatial positioning within the farm. As in Expt 1, water was pumped from a depth of 4.5 m to the surface inside the tube. The lice barriers were maintained for 55 d.

Each sea-cage was stocked with approximately 1400 Atlantic salmon (Aquagen strain; mean ± SE weight 1.45 ± 0.2 kg) size. Fish in all cages underwent topical chemotherapeutant bathing (ALPHA MAX®, Pharmaq; www.pharmaq.no) to remove salmon lice before the experiment commenced. Fish were fed daily by hand with 9 mm Skretting Spirit pellets (Skretting) following standard production procedures as in Expt 1.

2.2. Salmon lice sampling

As louse development is temperature-dependent (Samsing et al. 2016), and the average water temperatures fish would have experienced differed between Expts 1 (16°C) and 2 (5–10°C), we sampled at different intervals. In Expt 1 (16°C), at intervals of 16–24 d (Periods 1–4), 20 fish from each cage were captured, anaesthetised with tricaine methanesulfonate (100 mg l^{-1}; Finquel, Western Chemical), and the number of lice counted. Lice were categorised as chalimus (I-II), pre-adult I, pre-adult II or adult stages. Chalimus and pre-adult I stages that were detected on fish at the end of each of Peri-

ods 1–4 could be definitively attributed to infestations that occurred during that period, as these lice were less than 2–3 wk old based on the observed water temperatures and documented development rates (Johnson & Albright 1991). Only the pre-adult II and adult stages could not be assigned to a specific period. Between Periods 2 and 3 on experimental Day 42, fish in all sea-cages were treated with azamethiphos (Salmosan, FishVet Group) to remove lice, as adult lice abundance per fish in control cages exceeded levels that triggered mandatory delousing according to Norwegian legislation. In Expt 2 (5–10°C), at the end of the 55 d experimental period, 20 fish from each cage were randomly selected and the number of lice counted. As fish swam deep in this experiment, the temperature they experienced (7–10°C) for most of the time could lead to lice reaching the adult stage within the study period (Hamre et al. 2019).

2.3. Environmental measurements

Throughout Expt 1, daily environmental profiles of salinity and temperature were measured, and in Expt 2, daily environmental profiles of temperature, salinity, and oxygen were measured from the surface to 12 m depth at a reference point between all 6 experimental cages using a CTD (data collected at 1 s intervals; SD204, SAIV AS; www.saivas.no). In Expt 2, water transparency was also recorded daily using a Secchi disc. Measurements were taken after the morning feed event within the space of 1 h to minimise potential differences in natural environmental fluctuation.

2.4. Salmon swimming speeds, schooling and surface behaviours

Swimming speeds and group structure of fish were monitored with underwater cameras (Orbit 3000, www.orbitgmt.com) positioned in the middle of each cage, and reference lines were hung within the cage. Cameras were controlled by winches and were positioned at the centre depth of the school's vertical distribution during each sampling period. Videos lasting 5 min were recorded during the day in each cage, and from the video recordings, instantaneous swimming speeds were calculated in body lengths per second (BL s^{-1}) by measuring the time taken between the snout and the tail of a fish passing the vertical reference line (Dempster et al. 2008). The first 30 fish to pass within 1 m of the vertical reference line in each 5 min recording were used for this analysis. In Expt 1, swimming speeds were measured on 5 random occasions during the 76 d trial. In Expt 2, swimming speeds were measured every 2–4 d. In both experiments, recordings were made between 10:00 and 11:00 h when fish were visibly settled and no longer had a strong response to feed provision.

To derive a relative index of schooling, we used the variances of the 30 swimming speeds recorded in each sampling period (Dempster et al. 2009). This produced a relative index of the variability in swimming speeds among the 30 individuals measured; the lower the average variance, the lower the variability in the swimming speeds of the 30 fish, which is indicative of greater schooling.

In Expt 2, we also monitored surface behaviour in addition to swimming speeds and group structure. When the cage surface was broken by the fish — either gently with their snout, rolling through with a larger body proportion, or leaping — this was considered a potential swim bladder filling behaviour (Korsøen et al. 2012) and hereafter termed 'breaching'. To compare the extent of breaching in snorkel and control cages, the number of breaches observed in the cages was counted over a 5 min period on days when swimming speed measurements were taken. All counts were converted to breaches $fish^{-1}$ d^{-1}.

2.5. Vertical distribution of salmon and total echo-signal strength

In Expt 2, swimming depths of fish in 2 of the control cages and 2 of the snorkel cages were continuously recorded throughout the experimental period using a PC-based echo integration system (Lindem Data Acquisition; described by Bjordal et al. 1993). Transducers were positioned under the mid-point of cages at 17 m depth facing upwards with a 42° acoustic beam angle. Echo-intensities were recorded in 7 cm depth intervals, which were then converted into 1 m depth bands. A mean value of the echo observations per minute (60 pings min^{-1}) was recorded and used to calculate a relative density on a scale from 0 to 1. All data were condensed to hourly averages per 1 m depth interval prior to analysis.

The percentage of time fish spent swimming at different depths for Expt 2 during the 55 d period in which snorkels were in place was calculated in 1 m depth bands by averaging the total strength of echo-signals (TS_{corr}). This indicates where in the water column the highest density of fish was schooling (Oppedal et

al. 2007). TS_{corr} is indicative of the biomass that is present within the range of the acoustic beam; however, the collective volume of the fishes' swim bladders influences this value (Ona 1990). Thus, monitoring the total echo-strength over the experimental period can indicate whether the fish have been refilling their swim bladder or avoiding the snorkel (Dempster et al. 2009). Mean total echo for the snorkel and control cages was therefore calculated for each day of the experiment and compared to total echo before deploying the snorkel and after removing the snorkel.

2.6. Growth, condition, and feed conversion efficiency

For Expt 2, prior to the installation of the snorkels in treatment cages, sample groups of 100 randomly chosen individuals were captured with a 5 × 5 m cast net from each of the 6 cages and anaesthetised with tricaine methane-sulfonate (100 mg l^{-1}; Finquel, Western Chemical). They were then measured for weight and fork length, tagged with a uniquely numbered external T-bar anchor tag (30 mm, Hallprint; www.hallprint.com), and returned to their original cages after a period of recovery.

At the end of the trial, tagged individuals were retrieved from their cages, their tag number identified, and measured for weight and fork length. Fulton's condition factor (K) was calculated with the formula: $(WL^{-3}) \times 100$, where W is the wet weight (g) and L is fork length (cm). Specific growth rate (SGR; % d^{-1}) was calculated as $(e^q - 1) \times 100$, where $q = (\ln[W_2] - \ln[W_1])(t_2 - t_1)^{-1}$, where W_1 and W_2 are the body weights at the start (t_1) and end (t_2) of the trial, respectively. The feed conversion ratio (FCR) for each cage was calculated as feed (g) delivered per cage divided by the weight increase of the fish (g).

2.7. Snout wear and fin damage

In Expt 2, snout wear and fin damage were assessed for all tagged individuals. Snout condition was scored as 0 if no damage was evident, 1 for minor wear or damage, and 2 for severe wear or damage (see Stien et al. 2013). Dorsal and caudal fins were scored with an index from 1 (undamaged) to 5 (complete degradation) based on the method described in Hoyle et al. (2007). All condition measures were assessed by the same person. To investigate whether there were specific welfare issues associated with different fish sizes, the distribution of snout wear and fin damage across the size classes of experimental fish was described, whereby the frequency of snout wear and fin damage were plotted across the weight range of the sample group. Weights were categorised into 3 size classes: <2000 g, 2000–3000 g, and >3000 g.

2.8. Statistical analysis

For both experiments, differences in salmon lice numbers, average group swimming speeds, and average residuals between cages with and without lice barriers were tested for with a 1-way ANOVA, with $\alpha = 0.05$ set as the level of significance. In Expt 2, differences between mean values in the treatment and control cages of change in weight and K, SGR, FCR, fin and snout damage levels, swimming speeds before, during, and after the snorkel was installed, breaching behaviour, vertical distribution, and TS_{corr} were tested for with 1-way ANOVAs. Test assumptions (normality and homogeneity of variances) were evaluated by assessing residual plots. The frequency distribution of snout wear and fin damage (both caudal and dorsal) within size classes were compared between treatment groups with multiple chi-squared tests.

3. RESULTS

3.1. Expt 1: Coastal site with unsystematic halocline

Surface waters remained relatively well mixed throughout the 76 d experimental period (Fig. 1A). In Periods 1 and 2, salinities were 30–33 ppt for most of the time at all depths, except for some lower salinity events in the upper 1–2 m of the water column. In Periods 3 and 4, the water column fluctuated between unstratified, with salinities >30 ppt at all depths for periods of days, to stratified, with lower salinity waters (20–25 ppt) extended from the surface to depths of 3–5 m.

Sea-cages with lice barriers consistently reduced total salmon lice abundances relative to control cages (Fig. 1B) as evidenced by the lower abundances of chalimus I-II and pre-adult I stages (Fig. 1B; $p < 0.001$ in all periods), which infected salmon in the 2–3 wk prior to each sampling event. Salmon in cages with snorkels had 84, 71, 84, and 66% (mean reduction = 76%) fewer lice of the infectious stages in Periods 1–4, respectively, compared to control cages without snorkels. The differing levels of lice reduction did not

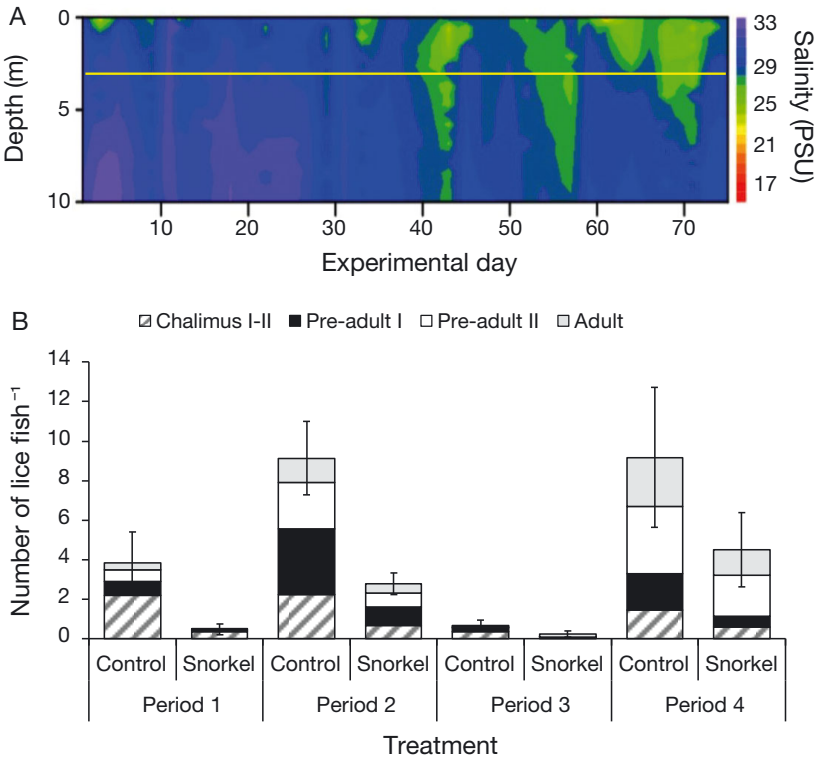

Fig. 1. (A) Continuously recorded vertical salinity profile of the water column from 0–10 m depth for Expt 1 conducted at a coastal site with an unsystematic halocline (Austevoll) over the 76 d experimental period. Solid yellow line: maximum depth (3 m) of the anti-lice barrier. (B) Mean (±SE) abundances of different developmental stages of salmon lice fish^{-1} for each period in Expt 1. Bars represent the mean of 20 Atlantic salmon in each of 3 lice-barrier or control sea-cages

directly correspond with the more unstratified water column in Periods 1 and 2. Despite a more stratified water column in Periods 3 and 4 where lower salinity waters (20–25 ppt) appeared in the upper 2–3 m of the water column, we did not observe higher lice levels as expected.

Average swimming speeds did not differ between the lice barrier cages (range: 2.10–2.24 BL s^{-1}) and control cages throughout this period (range: 2.14–2.68 BL s^{-1}; p = 0.22). No difference in the schooling index was detected (p = 0.6).

3.2. Expt 2: Fjord site with a strong halocline

Water temperatures of up to 5°C occurred in the first 12 m of the water column in the first 3 d (Fig. 2A). For the remainder of the experimental period, the upper 0–3 m had a dissimilar, cooler temperature (mean: 5.1°C; range: 3.2–6.0°C) than lower depths (mean: 7.1°C; range: 5.2–10.1°C; Fig. 2A). A distinct halocline existed at 3–5 m depth throughout the experimental period (Fig. 2A), with brackish, low-saline waters in the shallower waters above the halocline (mean: 24 ppt; range: 15–32 ppt), and stable salinities below it (mean: 32 ppt; range: 25–33 ppt). Mean (±SE) oxygen saturation levels were 105 ± 0.2% at the surface and 84 ± 0.1% in the 5–20 m layer (Fig. 2A). Water transparency averaged 14.9 ± 0.6 m during the experimental period and followed a seasonal pattern decreasing with the spring algae bloom, also seen in the pattern of algal oxygen production.

The presence of the barrier did not affect salmon lice infestations, with no difference in total salmon lice levels observed between snorkel and control treatments at the end of the trial (p = 0.7; Fig. 2B). All stages of salmon lice were prevalent on the salmon, with 0.6 ± 0.2 chalimus and 0.3 ± 0.1 pre-adult I lice fish^{-1}. Pre-adult II and adults were similarly abundant, with an average of 0.7 ± 0.3 and 0.6 ± 0.2 lice fish^{-1}, respectively. None of these stages differed in abundance between snorkel and control treatments (p > 0.49 in all cases; Fig. 2B).

Average swimming speeds were 1.14 times faster in the snorkel cages (range: 0.73–0.75 BL s^{-1}; Fig. 3A) than control cages throughout this period (range: 0.62–0.68 BL s^{-1}, p = 0.01; Fig. 3A). No difference in the schooling index was detected (p = 0.2). Surface behaviours were measured on 21 d during the experimental period (Fig. 3B) and ranged from 0.4–2.6 breaches fish^{-1} d^{-1} in control cages (mean ± SE: 0.99 ± 0.13) to 0–2.5 breaches fish^{-1} (0.39 ± 0.11) in snorkel cages. On average, fish in control cages exhibited surface behaviours 2.8 times more than fish in snorkel cages (p < 0.001; Fig. 3B).

Fish predominantly swam in the deeper and warmest parts of the cage in both control and snorkel cages throughout the experimental period (Fig. 4), spending 70% of the overall time in the 8–12 m depth range. Fish in the control cages spent only 9% of the time in the colder, brackish water layer from 0–3 m depth that the snorkel cages excluded fish from entering (Fig. 4).

Total echo-signal strength decreased by about 30% in the snorkel cages relative to initial values

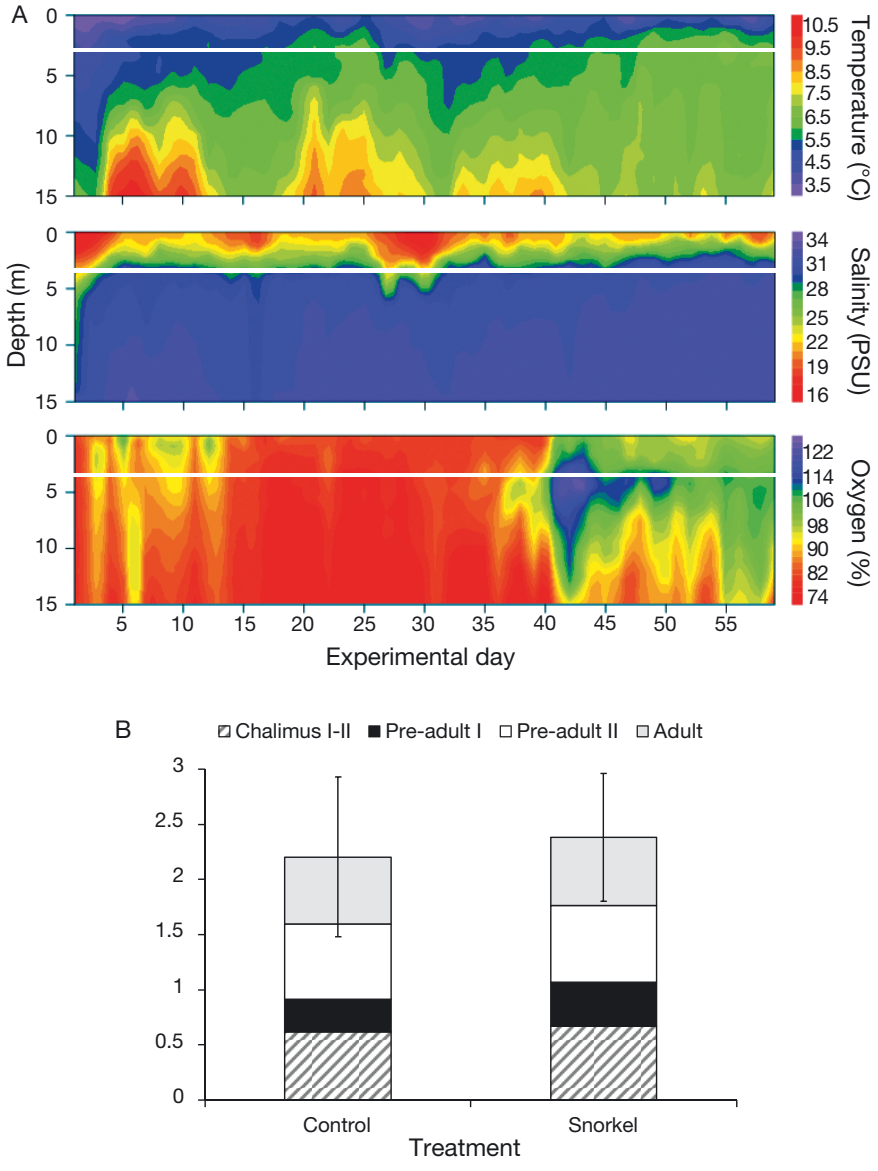

Fig. 2. (A) Continuously recorded vertical temperature, salinity, and oxygen profile of the water column from 0–10 m depth for Expt 2 conducted at a fjord site with a strong halocline (Matredal in Masfjorden) over the 55 d experimental period. Solid white lines: maximum depth (3 m) of the anti-lice barrier. (B) Mean (±SE) abundances of different developmental stages of salmon lice fish^{-1} at the conclusion of Expt 2. Bars represent the mean of 20 Atlantic salmon in each of 3 lice-barrier or control sea-cages

after 10 d, with a subsequent decrease to about 40% by Day 34, and total recovery to pre-experimental levels when full surface access was re-instated upon snorkel removal (Fig. 5). Control cages displayed swim total echo-signal strengths ranging from 90–180% of initial values, with a different pattern from the snorkel cages.

Fish in snorkel cages fed 1–2 m below the base of the snorkel at 4–5 m depth, whereas some fish in the control cages fed near the surface. Despite this difference in the position of feeding activity, we did not observe distinct differences in appetite or other aspects of feeding behaviour between the fish in control and snorkel cages. Overall, 14% more feed was provided to snorkel than control cages (Table 1). Growth, increase in *K*, FCR, or SGR did not differ significantly between cage types (Table 1, Fig. 6). Fish grew well in both treatments over the 2 mo period and their *K* increased by 0.09–0.1 compared to their initial *K* (Fig. 6). Mortality was ≤0.1% in both treatments, with 2 fish deaths in the snorkel and 1 in the control treatment.

Evidence of snout wear occurred on 77% of fish in the snorkel treatment, compared to 48% in control cages. Average snout condition was 1.65 times poorer in snorkel than control cages ($F_{1,4}$ = 47, p = 0.002; Fig. 6D). Fish in the <2000 g (χ^2 test, χ^2 = 19, df = 2, p > 0.001) and the 2000–3000 g (χ^2 = 47, df = 2, p > 0.001) weight range had more snout wear in the snorkels than the controls, while fish >3000 g showed no difference (χ^2 = 101.1, df = 2, p > 0.05). Caudal and dorsal fin damage did not differ between treatments (p > 0.05 in both cases; Fig. 6), and there were no differences detected in any of the size classes of fish between snorkel and control (χ^2 test, p > 0.1 in all cases). Fin scores averaged 1.5 for caudal and 2.5 for dorsal fins, judged on a scale of 1–5 (Fig. 6).

4. DISCUSSION

4.1. Effects of lice barriers on salmon lice infestation level

We have demonstrated that, by placing lice barriers in farmed salmon cages, infestations were reduced by 76% compared to control cages at an unstratified site. The most parsimonious explanation for

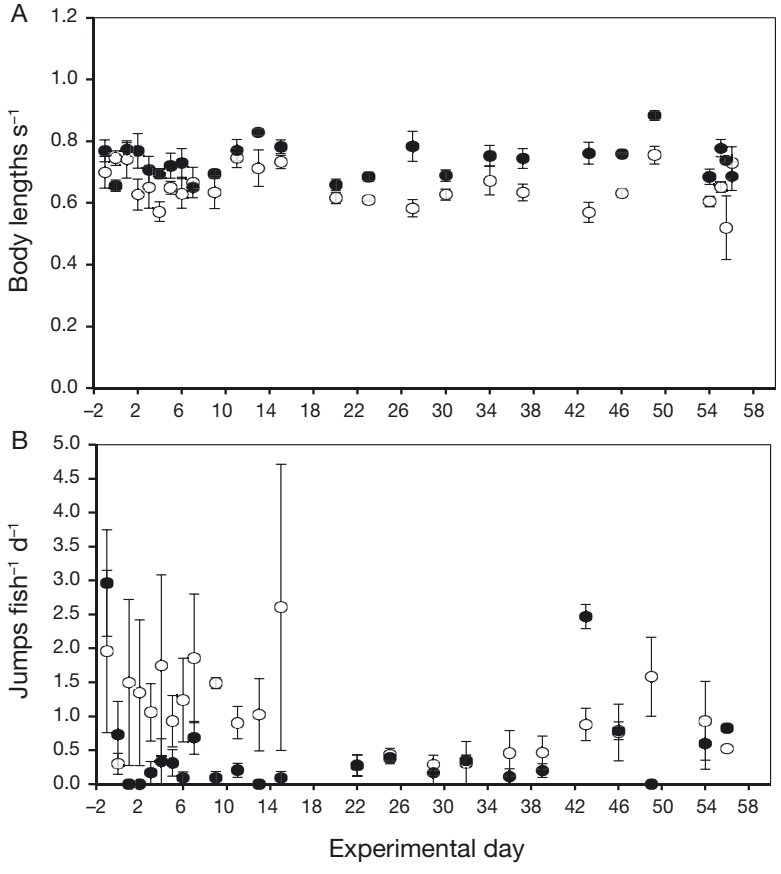

Fig. 3. (A) Swimming speeds and (B) breaches of Atlantic salmon in the control (○) and snorkel (●) cages over the 58 d experimental period for Expt 2. Each point is the mean instantaneous swimming speed of 30 fish

the strong and consistent effects observed in Expt 1 is that the lice barrier introduced a mismatch between host and parasite position in the water column and prohibited infestation within the central chamber when salmon sought to visit the surface. Combined, these effects reduced encounter rates and lowered infestation levels. In the coastal environment with a weak halocline, lice abundances were likely highest in the surface layer due to their positive phototaxis (Bron et al. 1993) and were similar to the results found in other snorkel experiments in coastal environments (24–65% less with 4 m deep snorkels, Stien et al. 2016; 84% less with 10 m deep snorkels, Wright et al. 2017). Our conclusion that the lice barrier created a spatial mismatch between salmon and infectious salmon lice copepodids is strengthened by the contrasting results of Expt 2. Here, we repeated the experiment in an environment with a strong halocline, with the low-salinity layer extending to depths below the bottom of the 3 m deep lice barrier. Infectious lice copepodids actively avoid salinities <30 ppt (Heuch et al. 1995, Crosbie et al. 2019), thus they were likely positioned deeper than the bottom of the lice barrier. Under these conditions, results reflected our prediction that lice levels per fish would not differ between lice barrier and control cages as host–parasite encounter rates are likely to be similar.

While differences in these experiments (season, fish size), do not make them directly comparable, combined, their results indicate the importance of the halocline depth and schooling depth with respect to infestation risk for salmon held in sea-cages. In Expt 2, fish in both cage types swam at similar depths of 8–12 m throughout the study period (Fig. 4) and thus would have had similarly limited interactions with the halocline, which was consistently present at around 4 m. Their similar infestation levels after 55 d strengthen the hypothesised significance of the halocline as a parasite-risky area. School swimming distance from the halocline was also found to be an important factor of susceptibility in commercial cages, whereby peaks of infestation in control cages were estimated to have occurred when the school was swimming within 5 m of the halocline (Bui et al. 2018). This relationship between host exposure to surface waters and susceptibility to infestation is further supported by the results of Oppedal et al. (2017), where infestation rates decreased exponentially with increasing barrier depth. Studies that have used depth-based pre-

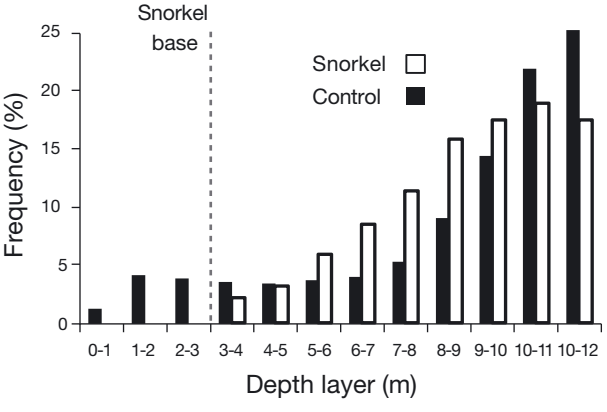

Fig. 4. Percentage of echo strength corrected for biomass (TS_{corr}) in Atlantic salmon by 1 m depth bands during the 55 d of snorkel installation given as means for the 3 snorkel and control cages for Expt 2. Dashed line: depth of snorkel cage roof, which was situated at the base of the snorkel structure

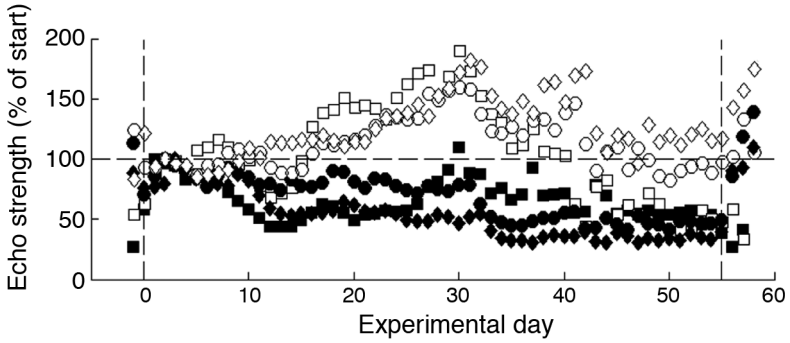

Fig. 5. Total echo strength corrected for biomass (TS_{corr}) in Atlantic salmon as a percentage of the initial total echo strength prior to snorkel installation given as means (±SE) d^{-1} for the 3 snorkel and control cages over the 58 d experimental period for Expt 2. Open symbols: replicate control cages; filled symbols: replicate snorkel cages

vention without a physical barrier to surface waters (e.g. deep lights and feeding) have not demonstrated as consistent an effect (e.g. Frenzl et al. 2014, Bui et al. 2018, 2019a), suggesting that the removal of exposure to surface water is essential for persistent effects. This could be achieved by using snorkels, lice skirts (Stien et al. 2018), or eliminating the potential interaction altogether via closed-containment cages (Nilsen et al. 2017).

4.2. Effects of lice barriers on salmon behaviour

The snorkel lice barrier separated salmon from the parasite-risky surface layer in the coastal environment with a weak halocline (Expt 1), while the fish were still able to access surface waters through a central chamber that was impermeable to parasites and express their natural swimming and schooling behaviours. While the lice barrier led to marginally increased swimming speeds (10% faster than controls in Expt 2), this effect was small compared to the 1.5–1.6 times faster swimming consistently observed when salmon are unable to access surface waters for an even shorter period (Dempster et al. 2009, Korsøen et al. 2009). With no ability to swallow air, fill their swim bladders, and maintain neutral buoyancy in the upper part of the water column, salmon compensate for negative buoyancy with elevated swimming speeds and hydroplaning (Dempster et al. 2008). As the lice barriers did not induce these strong effects, this indicates that salmon accessed the surface waters through the surface access tube with sufficient frequency to refill their swim bladders and maintain neutral buoyancy (see Fig. A1C in the Appendix).

In Expt 2, salmon lice levels were similar in snorkel and control cages. Therefore, we

Table 1. Production parameters for control and snorkel Atlantic salmon in Expt 2. No. of fish: mean number per treatment of stocked salmon; FCR: feed conversion ratio; *K*: condition factor. Values are mean ± SE. ns = no significant differences at $\alpha = 0.05$

Parameter	Control	Snorkel
No. of fish	1486^{ns}	1280^{ns}
Feed provided $fish^{-1}$ (g)	660	770
FCR	0.9 ± 0.10^{ns}	1.1 ± 0.06^{ns}
Initial *K*	1.12 ± 0.01^{ns}	1.16 ± 0.01^{ns}
Final *K*	1.22 ± 0.01^{ns}	1.25 ± 0.19^{ns}

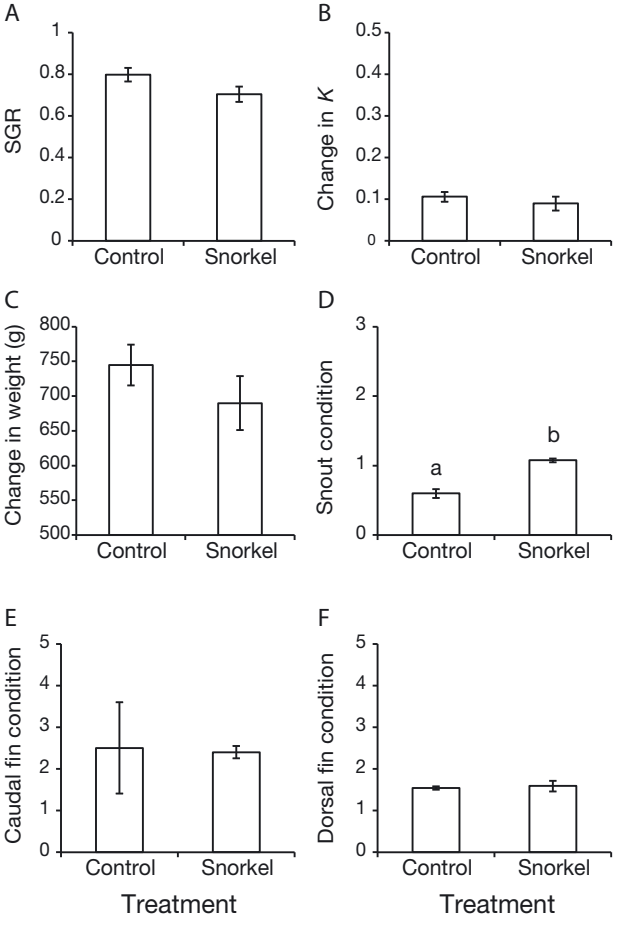

Fig. 6. Major production parameters for the control and snorkel cages housing Atlantic salmon at the end of the 58 d experimental period in Expt 2 showing (A) specific growth rate (SGR), (B) change in Fulton's condition factor (*K*), (C) change in weight, (D) snout condition, (E) caudal fin damage, and (F) dorsal fin damage. Each bar is the mean ± SE of 3 replicate cages per treatment. Different lowercase letters above bars indicate significant differences between treatments at $\alpha = 0.05$

were able to examine the effects of snorkel cages on salmon behaviour without the potentially confounding effect of different lice levels. Snorkel cages modified the swimming and breaching behaviours of fish relative to control cages, indicating a hesitation from the school to utilise the snorkel to access the surface. Compared to fish in the standard surface-based control cages, fish within snorkel cages exhibited marginally faster swimming, a lower overall level of surface behaviours, and a reduction in total echo-signal relative to the signal observed prior to snorkel installation, which is indicative of reduced swim bladder volume. Combined, these parameters indicate that snorkels reduced the frequency with which fish accessed the surface to refill their swim bladders, which led to a marginal increase in swimming speeds across the entire period and a burst of swim bladder filling behaviour when the snorkel was removed. Increased swimming speed likely compensates for some degree of negative buoyancy through the hydrodynamic lift that accelerated swimming provides (Sfakiotakis et al. 1999, Dempster et al. 2009). In fully submerged cages where no access to the surface is possible, the total echo signal declines quickly, indicating empty swim bladders, and swimming speeds increase by 1.5–1.6 times (Dempster et al. 2008, 2009, Korsøen et al. 2009). Relative to these effects documented for salmon in fully submerged cages, the effects on behaviour we detected in the snorkel cages were comparatively weak and are therefore unlikely to influence their welfare status.

Stien et al. (2016) found that total echo strength from fish within snorkel cages was similar through time, indicating that fish refilled their swim bladders continuously. Further, swimming speeds did not increase, which indicated that fish utilised the snorkel often enough to maintain their buoyancy. In contrast, in Expt 2 we observed salmon in control cages exhibiting breaching behaviour on average once per day, whereas fish within the snorkel cage breached less frequently. The amount of surface activity within the snorkel varied among observations, indicating that the spatial restriction within the snorkel structure, environmental conditions, or other inherent motivational factors (e.g. hunger state) may have influenced the level of expression of this behaviour. If the nature of this variation can be better understood, there may be an opportunity to modify environmental conditions within the snorkel or manipulate the behaviour of the fish themselves through other means (Dempster et al. 2011, Bui et al. 2013a,b) to increase the amount of breaching at the surface. Alternatively, salmon could potentially be acclimated and trained towards the snorkel, so they would perceive it as a standard cage structure and use it more naturally (Bui et al. 2019b). This may serve to increase swim bladder fullness and reduce the physiological driver for increased swimming speeds, thereby reducing some of the effects on production parameters observed.

4.3. Effects of snorkel cages on salmon growth, FCRs, condition, and fin and snout damage

As lice levels in Expt 2 were similar in control and snorkel cages, we tested for differences between snorkel and control cages in the absence of different salmon lice levels on production parameters. In general, salmon within the snorkel cages grew well and were in good condition, indicating that the technique has considerable promise at full production scale with further optimisation. While we hypothesised the effect of the snorkel would lie somewhere between fully submerged and regular surface-based cages, growth and swimming behaviour were more aligned with observations from regular cages.

While we did not detect significant effects for most of the production and welfare parameters typically used to assess salmon farming systems, our results need to be understood in the context of the experiment and its power to detect effects. New cage technologies must be assessed at a commercial scale to determine their relevance before full-scale trials at commercial facilities, where production volumes will range from 1000–14000 t yr^{-1}. Few trials to test the performance of new technologies relative to existing surface-based sea-cages have been conducted (although see Stien et al. 2018), as replicating at the cage level is expensive and difficult. In Expt 2, SGR (12.5%) and FCR (18%) were worse in control than in snorkel cages, but not significantly so. Effects of this scale could be commercially relevant; thus, further investigation is warranted despite the fact that we did not detect a significant difference in this experiment. A post hoc modelling exercise indicated that, with 1–2 more replicates with average values representative of the treatment groups, significant differences would have been detected at the $\alpha = 0.05$ level for SGR and FCR — suggesting that at n = 3 replication, the experiment is at risk of making a Type II error. Repeated, commercial-scale experiments with similar replication would enable analyses that resolve the Type II error issue.

In Expt 2, we found that average snout condition was 1.65 times poorer in snorkel than control cages.

Similarly, Stien et al. (2016) found that the percentage of fish with severe snout damage was higher in snorkel cages (31%) than control cages (21%). Several explanations exist to explain why snout condition differed between the snorkel and control cages, including (1) the snorkel cages provided more net structure area for salmon to encounter compared to the controls; (2) salmon actively sought the surface due to their slightly more deflated swim bladders and swam into the net roof; and (3) the combination of feeding at depth and in a confined area, due to the way feed was delivered, increased competitive interactions during feeding which led to snout damage. Snorkel cages increases cage structure (added net roof and snorkel surfaces) available for salmon to interact with by 30%. Assuming a linear relationship between amount of structure and fish contact with structure leading to snout damage, this difference would account for approximately half of the effect size we observed. If salmon actively seek the surface and thereby interact more with the net roof, this may further explain the greater level of net damage. Interactions with net roofs that can lead to snout damage can occur in fully submerged cages (Korsøen et al. 2009). Finally, while we have no evidence from this trial that feeding at depth at the base of the snorkel created greater scramble competition for food than feeding near the surface, we cannot rule out this possibility.

Despite the differences in snout condition, in general, salmon within the snorkel cages grew well and were in good condition, supporting previous findings (i.e. Stien et al. 2016, Wright et al. 2017) and indicating that the technique has promise at full production scale with further optimisation. Our results may indicate that closer husbandry is required for snorkel cages to ensure adequate provision of food, maintenance of the snorkel structure, and continuous observation of fish behaviour to monitor welfare status so that actions can be taken if unacceptable levels are reached.

5. CONCLUSIONS

Understanding the behaviour of hosts and parasites within culture settings can provide key insights into the development of strategic approaches to control significant parasite outbreaks. In the aquaculture of Atlantic salmon in sea-cages open to the environment, reducing host–parasite encounter rates through spatial mismatching of host and parasite substantively prevented infestation of farmed salmon by salmon lice in full-scale industrial aquaculture settings. However, we also identified that, under specific environmental conditions (i.e. deeper halocline), snorkel cages become ineffective in preventing salmon lice infestations. Therefore, understanding the hydrodynamics and environmental conditions of current and future salmon aquaculture sites is important when deciding if snorkel cages should be deployed.

The potential to mismatch hosts and their parasites in culture environments and reduce encounter rates is likely widespread across aquaculture, which has experienced a recent, rapid expansion in the number of species being cultured (Duarte et al. 2007). If the behaviour of parasites and hosts in marine production systems are understood, there is potential to manipulate these attributes to reduce the probability of infestation (Bui et al. 2019b). For example, several major fish parasites have specific depth-related infestation patterns. Copepodids of *Caligus rogercresseyi*, which are the main parasite of farmed salmon in South America, are most abundant in surface waters (Molinet et al. 2011), and the infectious stages of the skin fluke *Neobenedenia girellae* concentrate in surface waters where most infestations of farmed kingfish *Seriola quinqueradiata* occur (Shirakashi et al. 2013). Similar farm-scale manipulations to separate parasites and hosts and reduce encounter rates could be effective in preventing infestation, which could in turn reduce reliance on more environmentally risky technologies for combatting parasites (Urbina et al. 2019).

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Appendix

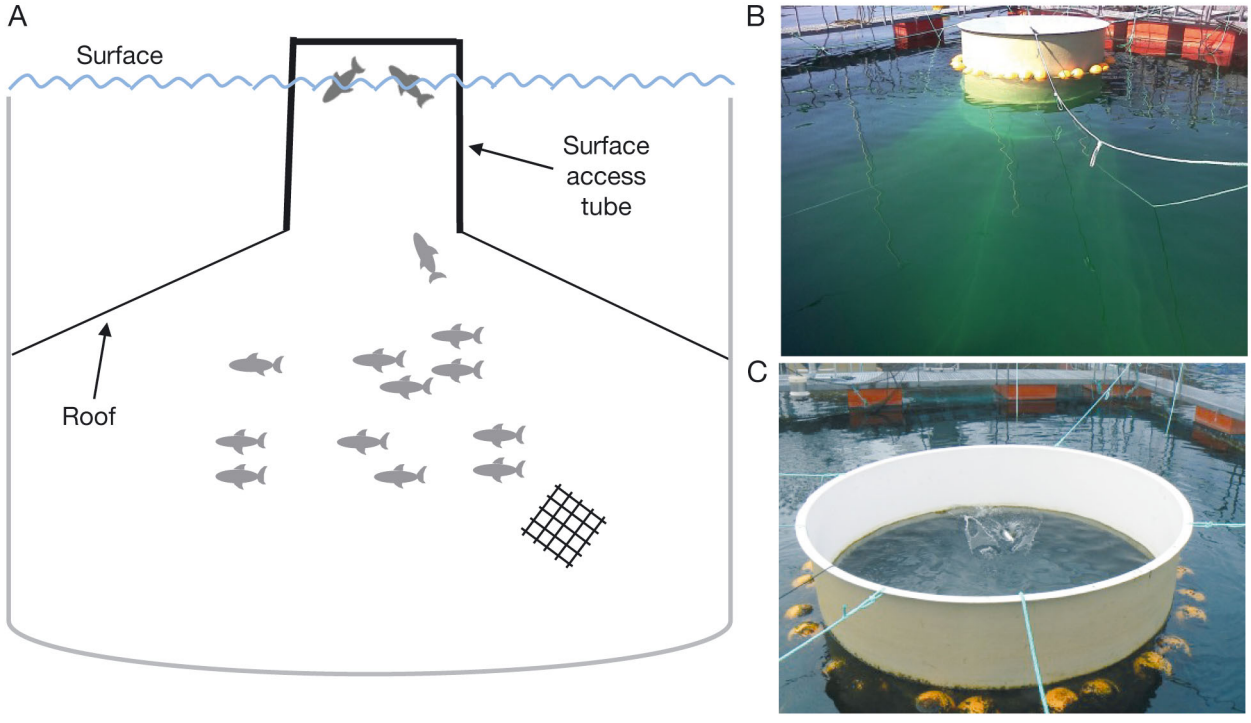

Fig. A1. (A) Schematic diagram of the central lice barrier installed in a standard surface-based Atlantic salmon sea-cage. Salmon can access the surface only within the area enclosed by the surface access tube ('snorkel'). (B) View of the lice barrier tube in position with roof netting visible below the surface. (C) A salmon rolling at the surface to refill air in the swim bladder within the surface access tube

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