Sea lice infestation levels decrease with deeper ‘snorkel’ barriers in Atlantic salmon
sea-cages

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ABSTRACT

BACKGROUND: Salmon lice (*Lepeophtheirus salmonis*) are the most important
parasite of farmed salmon. Infective larvae position themselves in the upper part of
the water column to increase encounter probabilities with potential hosts. Previous
studies have shown that a ‘snorkel’ sea-cage technology protects salmon from
infection in surface waters. We tested whether deep snorkels would more effectively
reduce lice infestation than shallow snorkels and still uphold adequate conditions for
the fish. Five sea-cages (12 m × 12 m) each holding approximately 3000 Atlantic
salmon (*Salmo salar*) (53 ± 10 g) were fitted with snorkels that gave protection from
infection for 0, 4, 8, 12 or 16 m. We tested if reductions in the settlement of new

This salmon lice copepodids were consistent among the 4 separate infection periods.
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RESULTS: Lice infestation decreased exponentially with depth in all time periods. Infection levels in shallow snorkels (0 and 4 m) were consistently four to ten times higher than those in deep snorkels (12 and 16 m). Key welfare and production performance indices were similar across all snorkel depths.

CONCLUSION: Deeper snorkels dramatically and consistently reduced infection levels of salmon lice compared to shallow snorkels without consequences for fish welfare and production performance. Therefore, reducing salmon sea lice encounters using a depth-based barrier is a powerful management tool for salmon farming.

Keywords: fish behaviour, *Lepeophtheirus salmonis*, parasite management, production parameters, *Salmo salar*, sustainable farming

1. INTRODUCTION

In the last four decades, sea-cage salmon farming has become an extensive, industrialized industry that accounts for 7% of all fish produced by aquaculture.¹ The subsequent increase of salmon hosts in the ocean fosters the proliferation of their parasites,² which negatively affect wild fish populations³⁻⁵ and may cause poor welfare and production outcomes for farmed fish.⁶ Ecto-parasitic salmon lice *Lepeophtheirus salmonis* (hereafter referred to as salmon lice or lice) are the most significant parasitic problem affecting salmon in the Northern Hemisphere.⁷ Sea lice control measures constitute more than 10% of productions costs⁸ and conventional drug-based treatments are becoming less effective due to the development of resistance.⁹ The reduced sensitivity of salmon lice to most available chemotherapeutants has led to the development and adoption of non-chemical

1 methods to remove or prevent lice infestations. Some of these include delousing
2 lasers, thermal/mechanical baths, cleaner fish ¹⁰ and depth-based lice-barrier
3 technologies. ¹¹⁻¹³ Cleaner fish can be effective against salmon lice, ^{14, 15} but they can
4 have poor welfare in net-pens, ¹⁶ they can become vector of other diseases, ^{17, 18} and
5 there is significant variation in their delousing ability in salmon net pens. ¹⁹ Limited
6 published data exists to assess the effects of lasers and thermal/mechanical baths on
7 both lice removal and welfare consequences for the fish, but reports from the industry
8 indicate that thermal baths have an increased risk of mortality. ²⁰ Overall, the effects
9 of preventive methods on both lice infestation and fish welfare are uncertain. Further
10 work is needed to develop preventive strategies to tackle salmon lice epidemics.

11 Understanding the behaviour of both salmon lice and salmon provides
12 opportunities to develop new approaches to prevent parasitic outbreaks. Free-living,
13 infective, salmon lice copepodids are phototactic larvae that have evolved to position
14 themselves in the upper part of the water column to increase encounter probabilities
15 with potential hosts. ^{21, 22} By exploiting this aspect of their behaviour, a possible
16 solution is to prevent or limit the contact of sea-caged salmon with surface waters.
17 Mismatching host-parasite encounters is the principle behind most depth based lice-
18 barrier technologies such as fully enclosed floating tanks where the water is pumped
19 from the deep, ¹³ cages that incorporate plankton-shielding skirts ^{23, 24} or lice 'snorkel'
20 barriers ¹¹ that stop encounters in surface waters, and fully submerged cages. ²⁵

21 Snorkel lice-barrier technology is a modification of a standard sea-cage where
22 salmon are held deep via a net roof, but allowed surface access to refill their open
23 swim bladders with air through a tube or snorkel. ¹¹ In previous experiments, a 4-m-
24 deep snorkel successfully reduced lice infestation levels, while retaining normal fish
25 behaviour and production performance. ^{11, 26} The effectiveness of this lice-barrier,

however, depends upon environmental conditions^{11,27} and the vertical position of fish in the water column.¹¹ In Dempster et al.²⁷ the snorkel cage did not reduce lice infestation compared to a standard control cage due to a persistent halocline at the same depth of the snorkel. In that experiment, lice copepodids, which actively avoid low salinity levels,²⁸ probably remained below the level of the snorkel and were able to infect the fish. In Stien et al.¹¹ the reduction in new lice infections (24 – 65% reduction) was not as pronounced as in Oppedal et al.²⁶ (66 – 84%) due to differences in environmental variables that influenced the position of control fish and lice larvae in the water column. In Stien et al.¹¹ periods of warmer temperatures deeper in the water column stimulated deeper swimming in the control fish, and evidence of water mixing may have transported lice larvae below the level of the snorkel,²⁹ decreasing the magnitude of its effect.

Evidence from previous experiments clearly suggests that the effectiveness of lice-barrier technologies may increase with depth. Therefore, we tested whether deep snorkels and hence greater salmon swimming depths would be more effective than shallow snorkels in reducing lice infection, while upholding adequate conditions for the fish. The present experiment was conducted in a fjord-coastal area in southwest Norway during autumn-winter, which is generally a critical infection period due to higher abundances of lice larvae in the environment.³⁰⁻³² Specifically, we tested the effect of increasing snorkel depths on parasite loads, fish welfare and fish growth parameters.

2. MATERIALS AND METHODS

All trials were conducted at the Institute of Marine Research aquaculture station in Austevoll, Western Norway (60.0° N, 5.3° E). The sea-cage facility at the station has steel cages in two rows across the tidal current directions (East-West, and West-East).

2.1. Pilot study

A pilot study was conducted in early summer (July – August 2014) using a standard sea-cage (12 m × 12 m, 21 m deep net), but with a net roof at 16 m and a tarpaulin tube (snorkel) from the center of the roof to the surface (3.2 m² at surface and 3 m diameter at roof depth). The purpose of this pilot study was to get practical experience with the handling of this snorkel cage and to confirm that fish could adapt to the technology. We observed that salmon used the snorkel to re-fill their swim bladders, displayed normal behaviors for a sea-cage environment and had similar growth rates to a group of fish kept in a neighboring unmodified sea cage (5 m × 5 m × 7 m). Salmon lice infection levels were reduced by 99% in the cage with the 16 m deep snorkel (0.2 ± 0.5 lice fish⁻¹; mean ± SE, all lice stages) compared to the standard cage (27 ± 8 lice fish⁻¹, all lice stages).

2.2. Experimental set-up and design

The main experiment was conducted between November 2014 and February 2015 using five randomly distributed sea-cages (12 m × 12 m) with net-roofs at 0, 4, 8, 12 or 16 m and snorkels from the roofs to the surface (Fig. 1). Each cage had 5 m deep swimming areas beneath the roofs. The snorkels were tarpaulin-enclosed square tubes (3.2 m² at surface) placed in the middle of the cages that extended from the surface down to the corresponding depth. Fish could only access the surface through an opening in the net roof and swimming up the respective snorkel.

Each snorkel cage was stocked with ~3000 Atlantic salmon (*Salmo salar*, autumn transferred smolts, Aquagen strain, Aqua Gen AS, Trondheim, Norway) with an initial mean weight of 53 ± 10 g (mean ± SD) at sea transfer. Throughout the experimental period, fish were fed in excess via a hose distributing the feed at the surface within the snorkel. To maintain oxygen levels within the snorkels, a

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continuous flow of water from below the snorkel edge was distributed to the snorkel surface area using an electrical water pump. The pump distributed 80 l min⁻¹ inside all snorkels, but was increased to 180 l min⁻¹ in the 16 m snorkel cage a week after fish were transferred to each sea-cage to ensure adequate oxygen levels.

2.3. Environmental conditions

Throughout the experimental period, environmental profiles were collected for temperature, salinity and oxygen at one reference point in the center of the farm between all experimental cages using a CTD (SD204, SAIV AS, Bergen, Norway, www.saivas.no) from the surface to 22 m depth. Oxygen levels inside the snorkels were measured once per week (SD204 with SAIV205 DO probe), and **within 24 h profiles were taken during the day and during the night.**

2.4. Sampling of individual fish

Every three weeks (sampling points 1 – 4: December 2 and 18 2014, January 13 and February 3 2015) 20 fish were randomly netted from each snorkel cage, and killed with a rapid blow to the head. Sampled fish were assessed for both salmon lice infection levels and fish welfare according to the Salmon Welfare Index Model 1.0 (SWIM 1.0).³³ SWIM 1.0 aggregates welfare indicators such as condition factor, fin condition, skin condition and lice levels, into an overall welfare index (OWI) for each individual fish, from 0 (worst) to 1 (optimal). In this trial, lice levels were not considered for the calculations of the OWI.

For each individual fish, the number of attached lice were counted and classified according to life stage into: chalimus I, chalimus II, pre-adult I, pre-adult II (male and female) and adult (male and female with or without egg strings). This was used to calculate the mean number of lice per fish (lice abundance), and prevalence

(proportion of infected fish). The infection rate was calculated using the number of newly attached lice (i.e. non-adult stages) for each sample period for comparisons among groups.¹¹ It was assumed that non-adult stages counted at the end of each sampling period had settled during that sampling period, based on the temperature-dependent development times of salmon lice.³⁴

2.5. Growth, condition and mortality

A week before sea transfer (week 0), 100 fish from each group were randomly captured and anesthetized with Finquel® (tricaine methane-sulfonate, Western Chemical; dose 100 mg l⁻¹ of seawater) to measure weight and fork length, tagged with uniquely numbered external T-bar anchor tags (30 mm, Hallprint, Australia, www.hallprint.com), and returned to their original groups after a period of recovery. At the end of the experiment, the tagged individuals were retrieved from their cages, and measured for weight and fork length. With these data, Fulton’s condition factor (K) was calculated as $WL^{-3} \times 100$, where W is the wet weight (g) and L is fork length (cm). Specific growth rate (SGR, % day⁻¹) was calculated for the 100-tagged individuals as $(e^q - 1) \times 100$, where $q = (\ln(W_2) - \ln(W_1))(t_2 - t_1)^{-1}$ and W_1 and W_2 are the wet body weights at the start (t_1) and end (t_2) of the trial, respectively. Mortalities were observed daily using the underwater cameras and retrieved three times per week with a cone-shaped fine net lying on the bottom of the cage.

2.6. Swimming speed and surface activity

Swimming speeds were monitored using submerged cameras (Orbit 3000, Orbit GMT AS, Førresfjorden, Norway) with pan/tilt to the depth of the school in each cage. Swimming speed measures were taken once a week during a non-feeding period at daytime throughout the trial. Swimming speeds were calculated as body lengths per

sec (BL sec^{-1}) by measuring the time taken for the snout and then the caudal fin to pass a vertical reference line within the cage.³⁵ Speeds were recorded for a total of 30 randomly chosen individuals: 15 individuals while the camera was facing west and 15 when facing east. This was to take into account any differences in swimming speeds due to the two main current directions.³⁶

To monitor swim-bladder refilling behaviour, surface jumping was measured on the same day that swimming speeds were monitored. A 'jump' was any surface activity when the fish either rolled at the surface or leapt above the surface. Jumps were counted over a 5 min period in each cage. All counts were converted to jumps $\text{fish}^{-1} \text{min}^{-1}$.

2.7. Statistical analyses

Data analysis was performed using R software Version 3.1.0 (Copyright 2009, The R Foundation for Statistical Computing, Vienna, Austria). Salmon lice infestation data (i.e. log-transformed number of newly attached lice per fish and log-transformed new lice prevalence) were analyzed using linear mixed effect models fit with restricted maximum likelihood (REML;³⁷), with depth as an increasing fixed effect and sampling period as a random effect (function 'lmer' in 'lme4' package, R). Mixed effects models with period as random effect were used to compensate for problems with pseudo replication from having four sampling points from the same cage.³⁷ In addition, regression models (function lm, R) for each sampling period were used to plot the relationship curves for each specific period and to compare total accumulated lice loads (log-transformed) on the last sampling. Mixed effects models were compared to corresponding null models excluding depth as a factor in likelihood ratio tests (function 'anova', R) to attain p- and χ^2 -values. We also conducted linear mixed effects analyses for welfare indicators in SWIM, jumping behaviour and swimming

speeds, but for the two latter with sampling week as random effect instead of sampling period. Cumulative mortality, change in weight, change in condition and SGR were analyzed by fitting linear regression models (function `lm`, R). Homogeneity of variance and normality of errors were confirmed with model checking plots (function `'plot'`, R). Aggregated values below represent mean $\pm$ standard error.

3. RESULTS

3.1. Lice infestation

New salmon lice infections decreased exponentially with snorkel depth in all sampling periods (Fig.2A; general model: new salmon lice = $e^{(2.0-0.9 \times \text{depth})}$, $\chi^2 = 44.9$, $p < 0.001$). There was a marked increase in new lice infections at sampling periods 3 and 4 compared to sampling periods 1 and 2 (model only including period 1 and 2 versus model only including period 3 and 4, $\chi^2 = 12.7$, $p < 0.001$). The proportion of infected fish (prevalence) decreased exponentially with increasing snorkel depth (Fig. 2B) (general model: prevalence = $e^{(6.1-1.1 \times \text{depth})}$, $\chi^2 = 14.1$, $p < 0.001$). Total accumulated lice loads (all lice stages at week 12 sampling) also decreased exponentially with depth (general model: total accumulated lice = $e^{(3.3-0.74 \times \text{depth})}$, $R^2 = 0.99$, $p < 0.001$). Final infection levels were 14.5 ± 1.0 (0 m snorkel depth treatment), 5.3 ± 0.6 (4 m), 3.5 ± 0.5 (8 m), 1.4 ± 0.4 (12 m) and 0.7 ± 0.2 (16 m) lice fish⁻¹. The average number of adult females were 2.20 ± 0.27 (0 m), 0.50 ± 0.14 (4 m), 0.35 ± 0.13 (8 m), 0.10 ± 0.07 (12 m), and 0.05 ± 0.05 (16 m). Accordingly, salmon kept near the surface in the 0 and 4 m snorkel cages had about 10 times more lice at the end of the experiment than the salmon kept in the 12 m snorkel cage and about 20 times more lice than salmon kept in the 16 m snorkel cage.

3.2. Fish welfare, growth and condition parameters

The amount of surface activity decreased with snorkel depth (general model: jumping = $0.39 - 0.25 \times \text{depth}$, $\chi^2 = 16.7$, $p < 0.001$) except for the 16 m snorkel cage, where jumping increased again (Fig. 2C). Swimming speeds were similar across all snorkel depths ($\chi^2 = 0.25$, $p = 0.62$) (Fig. 2D).

None of the individual welfare indicators in SWIM suggested a difference between snorkel depths, and the overall welfare index was therefore similar across all depths (Fig. 2E) ($\chi^2 = 0.7$, $p = 0.39$). Mortality in the 16 m snorkel cage was higher (4%) than for the other snorkel depths (0.3-1.6%) for the first ten days after sea transfer (Fig. 2F). From day 10 to day 90, mortality ranged from 0.16-1% across all snorkel depths with no clear depth-related pattern ($R^2 = 0.32$, $p = 0.32$). Moreover, there was no relationship between snorkel depth and change in weight ($R^2 = 0.007$, $p = 0.16$), SGR ($R^2 = 0.001$, $p = 0.56$) or change in condition K ($R^2 = 0.008$, $p = 0.13$). Fish in all snorkel cages had similar and adequate condition ($K = 1.16 \pm 0.01$) and SGR ($0.98 \pm 0.01 \text{ \% day}^{-1}$) for their size 12 weeks after sea transfer (Table 1).³⁸

3.3. Environmental conditions

Temperature was largely homogeneous with depth from 0 – 20 m in period one (Fig. 3; 10-12 °C), with a shift to colder temperatures in periods 2 and 3. By period 4, temperatures throughout the water column had dropped to 7 °C, with shallow pockets of colder water (2-5 °C) appearing sporadically in the surface waters. Throughout all 4 periods, salinity at all depths was generally high (>30 PSU), except for short episodes restricted to shallow depths in periods 1, 3 and 4.

Dissolved oxygen levels in waters within the 16 m deep snorkel were reduced compared to the others (Fig. 4A, B), even though additional water was pumped from beneath the snorkel edge into it. Conversely, in the shallow snorkels (8, 4 and 0 m

deep) the pump system maintained oxygen saturation at 90 % during daytime and above 75 % (Fig. 4A) at night (Fig. 4B).

4. DISCUSSION

4.1. Effect of snorkel depth on lice infestation

We observed a strong negative relationship between lice infestation levels and snorkel depth consistently across all time periods. Salmon kept near the surface had more lice than salmon in deeper snorkels. Lice infestation levels were 10 to 20 times lower in the deeper snorkels than in the treatment with no depth protection (0 m snorkel). This should translate into fewer delousing treatments throughout a typical 14-month production period in the sea. However, the number of lice fish⁻¹ on salmon kept in the deeper snorkels was not negligible and could eventually necessitate delousing treatment in a commercial setting. For example, in Norway, the legislated treatment threshold is 0.5 adult female lice fish⁻¹.³⁹ However, our study was done under trial conditions with small fish and thus fish density was only ~0.6 kg m⁻³ in a 12 m diameter cage, whilst in the industry densities can reach up to 25 kg m⁻³ in cages with typical diameters of 25-50 m. As lice infection success does not increase with fish density and higher densities dilute the number of lice per individual host,⁴⁰ we hypothesize that when deep snorkels are used in commercial cages with higher fish densities, the average number of lice per fish could be lower than documented here under similar conditions. This may also diminish the likelihood of both male and female lice being present on the same host, which may reduce reproduction success and ultimately may decrease the severity of lice epidemics.⁴¹

The exponential reduction of lice infection levels with depth has two important implications. Firstly, the decrease in lice infestation levels is less pronounced at

greater depths compared to the shallower snorkels (i.e. the curve is less pronounced). This suggests that to completely avoid lice infestation the snorkel barrier has to be very deep. Secondly, the exponential reduction means that the benefit of increasing snorkel depth decreases with depth. Moreover, it is reasonable to assume that the costs and difficulties of constructing, deploying, and maintaining snorkel cages and rearing fish in them also increase with depth. Therefore, since environmental conditions such as the presence and depth of a halocline, local current conditions and vertical turbulence will influence the effectiveness of this preventive strategy,²⁷ its application requires a detailed assessment of local environmental conditions to optimize the trade-off between lice reduction and increased operating costs.

Although the negative relationship between lice abundance and depth was conserved throughout the experiment, lice infection levels were higher in the third and fourth sampling compared to the first two (Fig. 2). Long-term time series of the epidemiological patterns of lice infestation indicate that salmon lice abundances on farmed salmon show significant geographical, seasonal and inter-annual variations.^{30, 32, 42} Seasonal variations are generally driven by fluctuations in water temperatures. High lice abundances in late summer and the start of autumn are associated with higher water temperatures and lead to higher infection success rates and shorter generations times.³⁴ However, the presence of a chalimus peak has also been reported in Scotland during winter when temperatures are typically low.^{30, 43} This winter lice pulse could be explained by a time lag between lice released from farms in autumn, or associated to lower predation rates of farm-originated lice copepodids by invertebrate predators (e.g., zooplankton and jellyfish) present in lower abundances during winter.

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Data from this experiment was used to validate the vertical distribution of lice copepodids predicted by an individual-based dispersal model.⁴⁵ For validation, lice abundance on fish swimming at different depths was used as a proxy of vertically distributed lice infection pressure. The dispersal model predicted an exponential decrease of lice copepodids with depth matching our empirical data. Moreover, the model simulation also revealed that hindering fish from swimming close to surface waters was an efficient way of reducing lice infection pressure in most locations, and demonstrated that this technology is widely applicable for lice prevention. However, as observed in previous empirical trials, the model simulation also suggested that the effectiveness of snorkel barriers depends on local environmental conditions. Overall, our results expand our understanding of lice biology, validate biological parameters used in lice dispersal modeling, and contribute significantly to the evidence basis of depth-based preventive lice management strategies.

4.2. Effect of snorkel depth on salmon behaviour, welfare and growth parameters

The behaviour of fish in the experiment was consistent with those described for farmed salmon.⁴⁶ We monitored swimming speed and surface activity as behavioral proxies of swim bladder refilling, and therefore appropriate use of the snorkel. Throughout the experimental period, observed daytime swimming speeds in all snorkel depths were within the normal range described for Atlantic salmon in sea cages from 0.8 to 1.6 BL per second,^{25, 35, 47-49} and there were no differences in swimming speeds among the different depths treatments. Swimming speeds stabilized after three weeks, which may reflect more structured swimming over time. A recent trial noted that the typical ‘donut’ shaped schooling structure of salmon in net pens develops one to two months after sea transfer (Glaropolous et al. *pers. comm.*).

Furthermore, surface activity decreased with snorkel cage depth until the 12 m deep snorkel cage and then increased in the 16 m deep snorkel cage. Decreased surface activity indicates a reduced frequency with which fish access the surface to refill their swim bladders. This could lead to negative buoyancy and faster swimming speeds to compensate,^{35, 48, 50} but we did not observe this behaviour in fish in the deepest snorkel cages, which suggests adequate buoyancy during the trial. The increased surface activity in the deepest snorkel cage suggests that fish had to refill their swim bladders more often to create more lift. This increased surface activity, however, could be due to some fish remaining closer to the surface due to the energy it requires to swim up and down a longer tube. To verify this we would have to monitor vertical behaviour of the fish during the day and during the night, inside and outside the snorkel using ultra-sonic techniques (e.g. echo sounders)⁴⁶ and cameras that film from different angles and in complete darkness. Preferably, individual tagging techniques should be used to investigate and ensure that all individuals are using the technology.^{25, 47, 51} Further monitoring of fish behaviour in snorkel cages is an important consideration for future trials.

In general, salmon in the different snorkel cages grew well and were in good condition. Growth rates in all treatments were within values of 0.9 to 1.1% day⁻¹ as expected for the size of tagged fish we used in the trial and the sea temperatures during the first 12 weeks after sea transfer.³⁸ Moreover, all fish had adequate welfare scores based on the semantic model SWIM.³³ The only parameter that differed between cages with different snorkel depths was cumulative mortality during the first ten days after sea transfer. Fish in the deepest snorkel cage had twice the mortality than the other treatments groups in this period. This higher mortality may have been associated with stress and lower oxygen concentrations due to crowding of fish within

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the longer snorkel, but it declined after water exchange rate in that treatment increased. Therefore, after ten days there was no clear pattern between snorkel depth and mortality, and all snorkel cages had similar rates of mortality thereafter.

4.3. Snorkel environment and practical implications

Dissolved oxygen levels inside the snorkels decreased with the length of the snorkel barrier. Deeper snorkels contain a higher volume of water and thus a longer time is needed to exchange the water inside them and replenish oxygen levels. In addition, fish inside the longer snorkels have to swim longer distances to access the surface and thereby spend more time in depleted oxygen levels. In sea-cage environments, water quality is the result of local environmental conditions and farm specific characteristics.⁵² The main sources of new oxygen in marine environments are photosynthesis and the mixing of atmospheric oxygen, but these sources are insufficient to sustain the oxygen demands within salmon farms, and thus oxygen requirements must be met by physical transport (water currents). In salmon net pens, the physical transport of oxygen is limited by factors such as mesh size of the net walls, net fouling and local topography.⁵³ Similarly, longer snorkels restrict the normal flow and exchange of water is reduced with length.

The snorkel barrier technology can decrease lice levels at a commercial scale, but its use has to ensure adequate environmental conditions and water quality for the fish. In our trial, the main issue we encountered with deeper snorkels was lower dissolved oxygen levels. **However, future trials should examine water quality inside the snorkel in more detail, e.g. constant monitoring of oxygen, and levels of ammonia.** To increase water exchange and oxygen levels inside the snorkel we used water pumps, but the rate at which water was pumped was insufficient for the deepest snorkel. Therefore, to improve water quality, pumping rates could be increased or oxygen

could be incorporated in the form of hyper-oxygenated water or oxygen bubbling. Degraded water quality might lead to negative impacts on the fish if they reside in the snorkels for long periods, but shorter excursions to the surface, of seconds in duration, may not matter. However, fish generally avoid low water quality and may avoid low oxygen levels in sea-cages in specific environments.⁵³ Avoidance of the snorkel due to low oxygen could lead to a reduction in the frequency of access to the surface and thus reduced swim bladder filling leading to problems with buoyancy and swimming. Future management of water quality inside the snorkel should be balanced towards sufficient use by individual salmon using strategies to attract (light,⁵⁴⁻⁵⁶ feed,^{57, 58} water quality^{46, 59}) and deter (water quality,^{46, 59} underwater feeding^{46, 57}) fish to and from the snorkel, respectively. In addition, the supply of artificial oxygen or treatment of snorkel water has to be balanced with fish use and environmental oxygen thresholds to provide optimal conditions for feed intake and growth (e.g.⁶⁰).

Overall, the optimal depth of snorkels will depend on local environmental conditions at each farm. For example, sites near freshwater runoff with a marked halocline will require deeper snorkels to obtain optimal results, but sites with a more homogenous water column might not need the snorkels to be as deep. Further, deeper snorkels might be harder to operate and may prove infeasible for farms moored in shallow depths. Based on our results, the industry has already installed snorkels in several commercial scale sea-cages in Norway. Commercial-scale snorkels at present are 90 m in circumference and 10 m deep within sea-cages 160 m in circumference and 30-50 m deep.⁶¹ At these scales, current flow and oxygen flux will likely differ to our trial results, and therefore full commercial scale testing of the technology in different production environments is essential to determine the practical implications of operating these cages.

4.4. Conclusions

Our study highlights the substantial potential for deeper snorkels to reduce lice infestation to low levels, while still upholding adequate production and welfare conditions for the fish. The use of this technology could reduce the frequency of costly chemical delousing operations and alleviate the negative impacts associated with lice epidemics. By reducing the use of chemotherapeutants, the development of resistance could be mitigated or delayed.⁹ Moving from research to commercial scale will require solving numerous technical and practical challenges, and include testing the capacity of large salmon to cope with deeper snorkels. The use of depth-based technologies to prevent parasite infection can fundamentally alter the future of salmon farming by improving the sustainability of the industry.

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Figure 1. Experimental design. The net-roof of the lice-barrier preventive technology or 'snorkel' sea-cage technology prevents fish from accessing surface waters except via a vertical tarpaulin-lined chamber or snorkel impermeable to salmon lice larvae, suspended in the middle of the cage. This technology prevents fish contact with surface waters where infective salmon lice larvae are most abundant. The length of the central chamber or 'snorkel', and the depth of the sea-cage determined the swimming depths of the fish; all cages were extended 5 m under the net-roof to provide the same swimming volume for each group. The rectangle in the left corner shows the random interspersed of the different snorkel depths at the research farm.

Figure 2. Lice infestation levels (A,B), fish behaviour (C,D) and fish welfare (E,F). A) Average number of new lice infections per snorkel depth for sampling 1-4 (S1-4). Grey curves indicate modeled relationships between snorkel depth and new salmon lice infections per sampling period. B) Average proportion of fish infected (prevalence) with new lice per snorkel depth for sampling 1-4 (S1-4). Grey lines indicate modeled linear relationships between prevalence and depth per sampling period. Model coefficients (intercept and slope) for each sampling period were used to plot the curves. C) Surface activity (jumps fish⁻¹ min⁻¹) and D) mean swimming speed (BL sec⁻¹) per snorkel depth. The circles are ordered from left to right according to measurement week, and the first week is a closed circle for easy identification. E) Boxplots of welfare indexes calculated for the fish sampled from the snorkels of different depths aggregated for all samplings. F) Accumulated numbers of mortality in the snorkels of different depth.

Figure 3. Environmental conditions (temperature and salinity) throughout the experimental period measured at a reference point in the center of the farm. Vertical dashed lines indicate the end of the four lice sampling periods. The experiment started on November 10, 2014 and finished February 6, 2015. The gap in the data between days 55 and 64 was due to technical problems with automatic profiling winch caused a storm.

Figure 4. Average dissolved oxygen (DO) levels inside the snorkels during A) daytime and B) night. Lines represent the different snorkel depths. Dashed line = 16 m, dotted line = 12 m and continuous lines from left to right = 8 m, 4 m and 0 m, respectively.

Table 1. Growth and condition parameters for all snorkel depths.

Snorkel depth (m)	<i>n</i> fish	Change in weight (g)	SGR (% day ⁻¹)	Initial <i>K</i>	Final <i>K</i>	Change in <i>K</i>
0	81	86 ± 3.2	1.03 ± 0.02	1.14 ± 0.01	1.18 ± 0.02	0.04 ± 0.02
4	81	70 ± 3.8	0.90 ± 0.03	1.18 ± 0.01	1.17 ± 0.01	-0.02 ± 0.02
8	84	91 ± 3.7	1.09 ± 0.03	1.16 ± 0.01	1.18 ± 0.01	0.02 ± 0.01
12	77	82 ± 3.6	0.97 ± 0.03	1.15 ± 0.01	1.15 ± 0.01	-0.01 ± 0.01
16	81	73 ± 2.9	0.96 ± 0.03	1.16 ± 0.01	1.13 ± 0.01	-0.03 ± 0.01

Values are mean ± SE.

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