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Salinity and temperature alter the efficacy of salmon louse prevention

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ABSTRACT

Several promising preventive tools and strategies have been developed to combat infestation of salmon in marine cages by parasitic salmon lice. While most of the prevention strategies tested have significantly reduced louse infestations in some trials, they have also had negligible impact in others. To better understand the observed performance variability a meta-analysis was conducted to examine the efficacy of physical barriers and behavior modification, the louse prevention tools with the strongest evidence base, in relation to local salinity and temperature conditions. Integrated prevention strategies which combine behavior modification with skirt barriers gave the most consistent protection, halving louse infestations through all measured environmental conditions with no negative impacts on growth or gill condition. Snorkel barriers provide the greatest potential protection from lice, with reductions of over 80% in ideal conditions when salinity is uniform throughout the water column, but are sensitive to environmental variation and accompanied by reduced growth and increased amoebic gill disease severity. Behavior modification alone did not significantly impact louse infestation, growth or gill health in any conditions. The results herein show that understanding the interrelationships between preventive tools and environmental conditions is central to optimizing tool choice and deployment strategy. Parasite prevention does not operate in a vacuum, and clear understanding of the risks and limitations of such tools is critical for them to have practical applicability.

1. Introduction

Reactive treatment to remove parasitic lice (*Lepheotheirus salmonis*) from farmed Atlantic salmon has been the norm for decades. Overreliance on medicinal treatments resulted in the widespread development of resistance to >80% of currently available chemotherapeutants (Coates et al., 2021b). In response, risky, non-medicinal delousing treatments rose to prominence (Overton et al., 2018; Oliveira et al., 2021). Now the salmon louse population is larger than ever and delousing treatments are the single greatest threat to farmed salmon welfare (Sommerset et al., 2021). The reactive paradigm has failed (Fjørtoft et al., 2021).

Proactive prevention to reduce louse infestations, on the other hand, has received relatively little attention (Barrett et al., 2020a). While reactive delousing removes lice after they have located a host and potentially reproduced, preventive strategies target the pre-infestation phase by reducing encounter rate and/or infection success. By reducing infestation rate preventive strategies break the link between host and parasite, not only lessening current louse levels but also disrupting louse population dynamics (Jeong et al., 2021). A variety of salmon louse prevention strategies are in development, each with clear strengths and weaknesses (Barrett et al., 2020a; Guragain et al., 2021). The strategies with the strongest evidence base are barrier technologies, which aim to reduce the host-parasite encounter rate by minimizing the flow of infective lice through cages, and behavior modification which harnesses the environmental preferences of salmon and lice to reduce their spatial overlap.

Barrier strategies have shown the greatest potential effect, providing a median reduction in louse infestations of 78% over 13 trials; unfortunately, the effect is highly variable (Barrett et al., 2020a). Snorkel cages, which force the fish to be submerged except within a small tube encircled by a barrier, provided a median reduction of 76%, but range from an 8% increase to 95% reduction in the nine available studies (Oppedal et al., 2017, 2019; Barrett et al., 2020a). Similarly, skirts, where a barrier is wrapped around the uppermost portion of the entire cage, are moderately effective but more consistent, providing a median reduction in louse infestations of 55% (Grøntvedt et al., 2018; Stien et al., 2018; Barrett et al., 2020a). Behavior modification strategies, which use the position of feed dispersion and/or lights to lure salmon away from the depths where lice are expected to be at highest density, were highly effective in some situations but not others. At best, behavior modification reduced louse infestation by 93% compared to control

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cages, but at worst led to an 72% increase (Barrett et al., 2020a). It is clear that each of these strategies hold promise as louse prevention tools, however it is also clear that none of them are being deployed to optimal effect.

Throughout the early design phase of the barrier and salmon behavior modification strategies it was widely thought that copepodids, the infective stage of lice, were strongly influenced by light (Heuch et al., 1995). As a result barriers were designed to minimize the flow of surface water through cages, while feed dispersal and light position were shifted from the surface to submerged positions to lure salmon deep. Recent experiments have shed new light, however, on the behavior of copepodids. Contrary to expectation, controlled experiments have shown that, (i) copepodids aggregate at the water's surface, irrespective of light, when salinity is uniform (Szetey et al., 2021), (ii) if salinity is not uniform, copepodids avoid the brackish layer and aggregate in the halocline (Crosbie et al., 2019), and (iii) temperature is not an important driver of copepodid behavior (Crosbie et al., 2020). Taken together, these findings indicate that salinity has important implications for copepodid distribution and must be considered in the design and deployment of preventive strategies intended to reduce salmon-copepodid encounter rates. Simply minimizing the interaction between salmon and surface waters is insufficient.

Further, although temperature is not an important determinant of copepodid distribution, it is a critical driver of salmon behavior (Johansson et al., 2006, 2009). The only daily occurrence which can drive farmed salmon to ignore temperature is hunger (Oppedal et al., 2011). If feed dispersal does not occur at the preferred swimming depth, salmon will alter their vertical position until satiated, after which they return to the depth with optimal temperatures (Juell et al., 1994; Oppedal et al., 2011). Reported preferred temperatures based on group behavior in open sea cages vary, however it is clear that: (i) salmon avoid temperatures >18 °C, and (ii) preferentially select the depth of warmest waters up to 14 °C (Oppedal et al., 2001; Johansson et al., 2006, 2009). As such, attempts to alter the swimming depth of salmon via food luring or the use of artificial lights can only be expected to perform well when temperatures are either uniform throughout the water column or the desired swimming depth of the salmon aligns with their preferred temperature.

The objective of this study is to examine the influence of salinity and temperature on the efficacy of snorkel cages, skirt barriers and behavior modification in relation to louse infestation, gill health and growth. By understanding the conditions in which each strategy performs well and those when they do not, preventive tools can shift from being conceptually interesting novelties of research to practically applicable strategies.

2. Methods

To evaluate the efficacy of louse barrier and behavior modification preventive methods we conducted a meta-analysis of published studies in the scientific and grey literature. Relevant studies were identified by searching ISI Web of Science and Google Scholar in September 2022 using the following search strings: *(skirt OR snorkel) AND (salmo*)* and *(light* OR feed* OR behav*) AND (salmo*) AND (lice OR louse OR salmonis OR caligus)*. We also found additional studies referenced within the articles returned by the search. The articles were then filtered for inclusion in the meta-analysis based on three criteria: a) measure of relative louse infestation densities for both test and control groups, b) inclusion of temperature and salinity data, and c) commercial scale trial. In total we identified three relevant studies on behavior modification using lights and/or feeding, five studies on snorkel barriers, one study on skirt barriers alone and two studies on the integrated use of skirt barriers in combination with behavior modification for inclusion in the analysis.

Effect size, here calculated as the response ratio (RR) of μT/μC,where μT is the test group response and μC is the control group response, was determined for each sampling point in each trial. To enable comparison across studies effect size was standardized using the natural log of the response ratio: LnRR = ln(μT/μC). Three response variables were included in the analyses, fish weight (*LnRR_growth*), amoebic gill disease (AGD) score (*LnRR_gill*) and mean number of attached lice per fish (*LnRR_lice*). To ensure that no bias was introduced because of differential use of cleanerfishes or delousing, only attached louse counts were included. Each preventive strategy was then categorized as one of three *treatment* groups (categorical 3 levels: behavior, skirt+ or snorkel). Two additional explanatory variables were derived from the salinity and temperature data. Because copepodids, the infective stage of salmon lice, actively avoid brackish water (Crosbie et al., 2019), a brackish layer was defined as salinities of 26 ppt or less at 3 m water depth. These data were used to create the variable *halocline* (categorical 2 levels: present or absent). Additionally, because temperature is the key determinate of salmon swimming depth in marine cages, the depth at which the temperature was closest to 14 °C (*depth nearest 14 °C*, continuous) was determined (Oppedal et al., 2011). Standard procedures for data exploration were followed to identify any outlying observations and test for collinearity between variables (Zuur et al., 2010).

To examine the influence of temperature and salinity on preventive tool efficacy, each response variable (*LnRR_growth, LnRR_gill* and *LnRR_lice*) was modelled as a function of *treatment, halocline* and *depth14C* using gaussian generalized linear mixed models (GLMM). Additional interaction terms included were *treatment x halocline* and *treatment x depth14C* to allow for different relationships between the environment and each preventive treatment group. To incorporate the dependency among measurements from the same trial, *trial* was used as a random intercept. The glmmTMB package (Brooks et al., 2017) in R version 3.6.1 (R Core Team, 2018) was used to fit all models. To test for a significant effect of preventive strategy on response variables we conducted one way *t*-tests on the RR data, where mean RR under the null hypothesis of no preventive strategy effect = 0.

3. Results

The nine studies included in the meta-analysis provided 254 comparisons between test cages equipped with louse prevention tools and control cages (Table 1). In total there were 27 comparisons where behavior modification alone was tested (termed: behavior), 175 where snorkel cages were tested (termed: snorkel) and 39 where skirt barriers were used in combination with behavior modification (termed: skirt+).

3.1. Salmon lice

Snorkel barriers reduced new louse infestations but varied widely in their effectiveness (Fig. 1). In 99 of 175 comparisons (57%) the cages equipped with snorkel barriers had fewer than half as many lice as control cages, and conversely, in 36 comparisons (21%) had similar or more lice. The protective effect of snorkel barriers was strongly influenced by both salinity and temperature, with median reductions in louse infestation of 49% when a halocline was present ($t_{30} = -3.7$, $P = 0.001$) compared to 59% when there was no halocline ($t_{145} = -10.3$, $P < 0.0001$). Similarly, snorkel barriers were predicted to reduce louse infestations by 76–81% when the temperature nearest 14 °C is in the surface, versus 43–53% when optimum temperatures are at 25 m (Fig. 1).

Behavior modification alone did not significantly reduce louse infestations in any of the measured conditions but appears to perform best when the temperature nearest 14 °C is in the surface (Fig. 1). In only 4 of 27 comparisons (15%) the cages utilizing behavior modification had fewer than half as many lice as control cages, and conversely, in 11 comparisons (41%) had similar or more lice. Although behavior modification provided a median reduction of 42% when a halocline was present ($t_8 = -1.9$, $P = 0.09$), and only 16% in the absence of a halocline ($t_{19} = 0.52$, $P = 0.61$), the limited amount of data available were insufficient draw any conclusions (Table 2).

Table 1
Median and mean response ratios (test/control group) for fish weight, AGD gill score and attached lice count for each prevention strategy both with, and without, the presence of a halocline.

Treatment	Halocline	N	Effect size (T/C) Weight median	Weight $\bar{X} \pm SD$	Weight t	Weight P	AGD score median	AGD score $\bar{X} \pm SD$	AGD score t	AGD score P	Lice median	Lice $\bar{X} \pm SD$	Lice t	Lice P	References
Snorkel cage	*present*	*30*	0.89	0.89 ± 0.19	−2.27	0.033	1.66	2.20 ± 1.93	2.41	0.025	0.51	0.68 ± 0.68	−3.71	0.001	Geitung et al. (2021), Bui et al. (2020), Geitung et al. (2021), Wright et al. (2017a), Oldham, T. (unpublished)
	absent	*145*	0.88	0.90 ± 0.23	−7.36	<0.0001	1.10	7.52 ± 47.8	2.78	0.006	0.41	0.75 ± 1.93	−10.32	<0.0001	
Skirt+	*present*	*12*	1.01	1.01 ± 0.16	−0.53	0.615	1.00	0.93 ± 0.17	−1.00	0.423	0.37	0.53 ± 0.44	−4.17	0.004	Oldham et al. (2022), Bui et al. (2020), Stien et al. (2018)
	absent	*27*	0.99	1.01 ± 0.19	−0.24	0.815	1.00	1.01 ± 0.38	0.36	0.727	0.44	0.48 ± 0.28	−6.15	<0.0001	
Behavior modification	*present*	*8*	0.94	1.05 ± 0.28	0.19	0.851	0.97	0.95 ± 0.07	−1.33	0.315	0.58	0.76 ± 0.55	−1.95	0.092	Nilsen et al. (2017), Bui et al. (2020)
	absent	*19*	0.95	0.99 ± 0.16	0.53	0.607	0.93	0.95 ± 0.28	−0.52	0.619	0.84	1.09 ± 0.60	0.52	0.613	

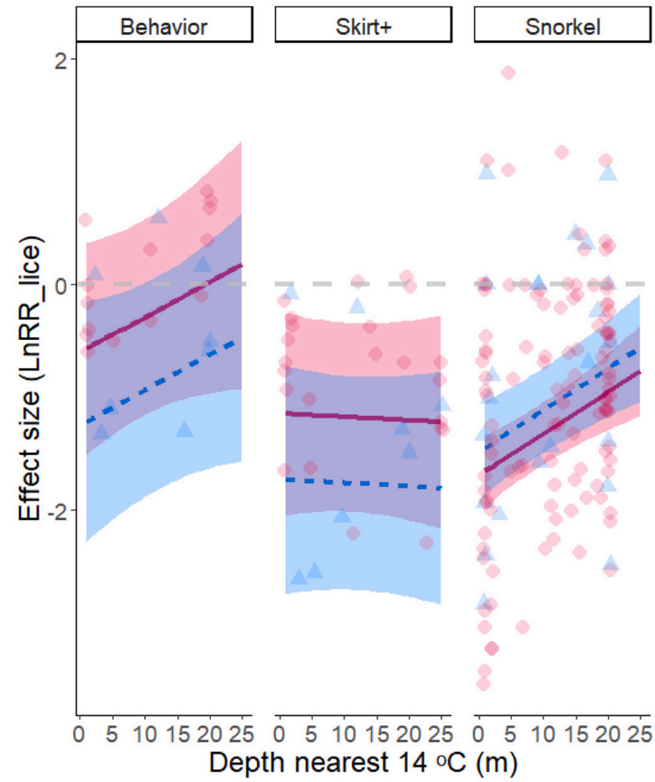

Fig. 1. Influence of temperature and salinity on lice preventive efficacy. Effect size (natural log of the response ratio: LnRR) of louse infestations as influenced by halocline (presence/absence), the depth of temperatures nearest 14 °C and preventive strategy. Colored lines and shaded areas display a fitted GLMM with 95% confidence intervals, while dot points represent each individual comparison. Red indicates no halocline, while blue indicates a halocline was present. LnRR = 0 corresponds to no difference between control and test groups (dashed grey line), while negative values indicate fewer lice in test cages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Skirt barriers used in combination with behavior modification tools consistently reduced new louse infestations both with a halocline present (median reduction = 63%, $t_{12} = -4.17$, $P = 0.004$), and without (median reduction = 56%, $t_{27} = -6.15$, $P < 0.0001$). In 25 of 39 comparisons (64%) the skirt+ cages had fewer than half as many lice as control cages, and conversely, in only 5 comparisons (13%) had similar or more lice. Temperature did not alter the preventice efficacy of the skirt+ strategy (Fig. 1).

3.2. Fish weight

Overall, fish in snorkel cag were smaller than fish in control cages (median reduction = 11%, $n = 175$; Table 1). Neither behavior modification alone (median reduction = 0%, $n = 27$) nor the skirt+ strategy (median reduction 5.5%, $n = 39$) affected fish weight (Table 1). Neither the presence of a halocline nor the depth nearest 14 °C, nor their interaction with any of the preventive strategies tested, significantly impacted fish weight (Table 2).

3.3. Gill condition

Fish in snorkel cages had higher AGD scores than fish in control cages (median increase = 38%, n = 175; Fig. 2). Compared to control cages, gill scores were worst in snorkel cages in the presence of a halocline (median increase = 66%, $t_{30} = 2.4$, $P = 0.025$) than without (median increase 10%, $t_{145} = 2.8$, $P = 0.006$). Neither behavior modification

Table 2
Estimate, standard error (SE), z-value and *p*-values of the explanatory variables in the models of (a) louse infestation, (b) fish weight and (c) gill condition.

	Estimate	SE	z	*P*
(a) New louse infestation				
Intercept	−0.239	0.411	−0.580	0.562
Treatment-Skirt+	−0.544	0.453	−1.201	0.230
Treatment-Snorkel	−1.088	0.495	−2.196	0.028*
Halocline-present	−0.645	0.381	−1.692	0.091
Depth 14 °C	0.031	0.023	1.381	0.167
Treatment-Skirt+: Halo-present	0.061	0.522	0.117	0.906
Treatment-Snorkel: Halo-present	0.851	0.430	1.979	0.048*
Treatment-Skirt+: Depth 14 °C	−0.034	0.028	−1.224	0.221
Treatment-Snorkel: Depth 14 °C	0.006	0.024	0.236	0.813
(b) Fish weight				
Intercept	0.056	0.096	0.581	0.562
Treatment-Skirt+	−0.137	0.121	−1.133	0.257
Treatment-Snorkel	−0.158	0.111	−1.428	0.153
Halocline-present	−0.003	0.104	−0.030	0.976
Depth 14 °C	−0.003	0.006	−0.446	0.656
Treatment-Skirt+: Halo-present	−0.016	0.141	−0.111	0.911
Treatment-Snorkel: Halo-present	0.025	0.117	0.216	0.829
Treatment-Skirt+: Depth 14 °C	0.006	0.008	0.838	0.402
Treatment-Snorkel: Depth 14 °C	0.000	0.007	0.031	0.975
(c) Gill condition				
Intercept	−0.063	0.484	−0.131	0.896
Treatment-Skirt+	0.096	0.634	0.151	0.880
Treatment-Snorkel	0.269	0.524	0.512	0.609
Halocline-present	0.006	0.630	0.009	0.993
Depth 14 °C	0.000	0.034	0.001	0.999
Treatment-Skirt+: Halo-present	−0.204	0.759	−0.257	0.797
Treatment-Snorkel: Halo-present	−0.077	0.656	−0.117	0.907
Treatment-Skirt+: Depth 14 °C	−0.001	0.038	−0.017	0.986
Treatment-Snorkel: Depth 14 °C	0.014	0.035	0.405	0.686

alone (median increase = 5%, n = 27), nor skirts in combination with behavior modification (median increase = 0%, n = 39), affected AGD score in any of the measured conditions (Table 2).

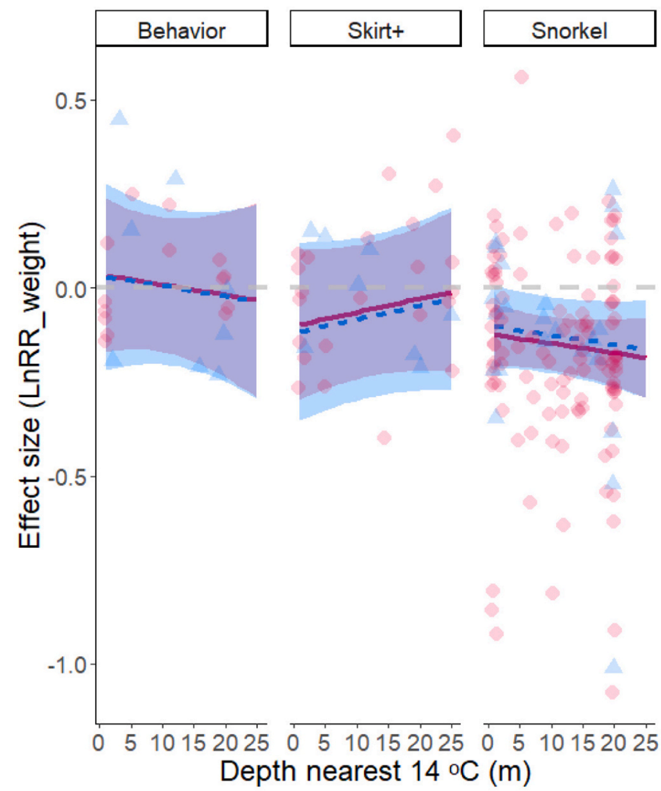

Fig. 2. Influence of temperature and salinity on fish weight when using preventive tools. Effect size (natural log of the response ratio: LnRR) of fish weight as influenced by halocline (presence/absence), the depth of temperatures nearest 14 °C and preventive strategy. Colored lines and shaded areas display a fitted GLMM with 95% confidence intervals, while dot points represent each individual comparison. Red indicates no halocline, while blue indicates a halocline was present. LnRR = 0 corresponds to no difference between control and test groups (dashed grey line), while negative values indicate smaller fish in test cages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Safe and effective prevention of louse infestations is possible in marine net cages, but not without holistic consideration of host and parasite behavior, local environmental variability and the strengths and limitations of the available prevention strategies. These results show that although there is currently no one-size-fits-all louse prevention solution, there are strategies available that can perform well on most farms.

4.1. Snorkel barrier

Given their potential to reduce louse infestations by >90%, snorkel barriers are an enticing option when only considering preventive effect. This 'best case scenario', however, only applies when salinity is homogenous throughout the water column and the depth of the salmon's preferred temperature is within the barrier. In other conditions the louse preventive efficacy rapidly declines (Fig. 1). Further, even when environmental conditions are favorable for louse prevention, use of snorkel barriers can lead to increased AGD severity (Fig. 3) and diminished growth (Fig. 2), despite reducing tapeworm infestations (Geitung et al., 2021).

There are several inter-related factors which can likely explain the strengths, and weaknesses, associated with the use of snorkel barriers. Unlike skirt barriers and behavior modification tools, snorkel barriers are fixed in place and require continuous aeration to ensure sufficient oxygen is available within the snorkel. When salinity and temperature are homogenous throughout the water column aeration can maintain oxygen levels and good water quality with no detrimental effects. However, when a halocline is present the pressure differential created by the aeration induced mixing causes the snorkel to deform in an hour-glass shape, similar to that previously described for skirt barriers (Jónsdóttir et al., 2022). The phenomenon has not been well documented, but observations suggest that the extent of hour-glassing is closely linked to three parameters: halocline strength, snorkel depth and aeration intensity. Deeper snorkels are more susceptible to deformation, with deformation being more extreme as halocline strength increases. In severe cases of hour-glassing the snorkel pinches closed and completely blocks surface access (Oldham, pers. comm.).

There are two potential options to remedy hour-glass deformation, (i) decrease or stop aeration output, and/or (ii) open surface 'vents' in the barrier to allow conditions within the snorkel to equalize with those outside the snorkel. Either way, there is no winning in such situations. When salinity is not uniform copepodids are deep, aggregating in the halocline (Crosbie et al., 2019). At the same time, hour-glassing means that the protective depth of the snorkel is reduced as the bottom ring of the barrier is pulled toward the surface. Leaving the snorkel deformed is not an option. Reducing aeration, however, is likely to result in rapidly decreasing dissolved oxygen within the snorkel, potentially to dangerous levels over-night. Finally, opening surface vents increases the likelihood of introducing copepodids directly into the snorkel. In some situations, if the brackish layer is strong or local lice pressure is low, opening vents can work well without negative repercussions. However, if the brackish layer is weak and causing deformation because the snorkel barrier is relatively deep (20 m +), or the deformation is due to a thermocline and salinity is uniform, opening vents, even briefly, can result in rapid louse infestations.

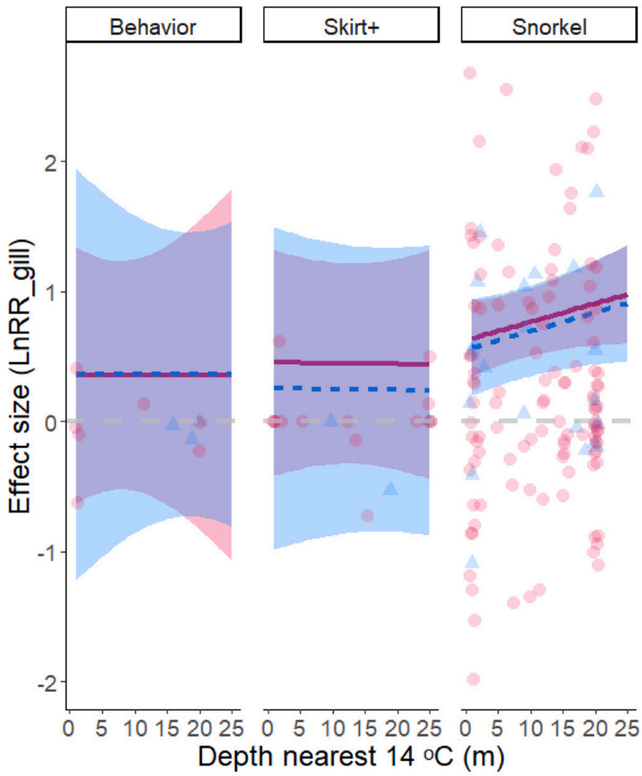

Fig. 3. Influence of temperature and salinity on gill condition when using preventive tools. Effect size (natural log of the response ratio: LnRR) of amoebic gill disease (AGD) score as influenced by halocline (presence/absence), the depth of temperatures nearest 14 °C and preventive strategy. Colored lines and shaded areas display a fitted GLMM with 95% confidence intervals, while dot points represent each individual comparison. Red indicates no halocline, while blue indicates a halocline was present. LnRR = 0 corresponds to no difference between control and test groups (dashed grey line), while positive values indicate higher AGD scores (worse gill condition) in test cages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Besides the challenges to growth and gill health which are obvious as a result of deformation challenges, there are additional concerns inherent with the use of snorkel barriers even when there is no halocline. Given the relatively small volume of snorkels in relation to the biomass of fish in commercial cages, even with continuous aeration dissolved oxygen concentrations fluctuate and can reach growth limiting levels (Oppedal et al., 2017, 2019; Wright et al., 2017a). The downstream effects of sub-optimal oxygen availability are numerous, but in connection with these data explain, at least in part, the reduced growth and elevated AGD severity observed in association with snorkel use (Remen et al., 2012; Oldham et al., 2019, 2020)

An additional factor which may contribute to the increased AGD severity observed in cages equipped with snorkels is 'self-treatment', or lack thereof. Because the amoeba which cause AGD are freshwater sensitive (Parsons et al., 2001), salmon in standard cages receive a sort of 'treatment' when they are lured into the surface brackish layer to feed throughout the day (Wright et al., 2017b). In snorkel cages, however, the aeration induced mixing can push full salinity seawater into the snorkel destroying the brackish layer. Consequently, fish in snorkel cages do not receive the natural benefits of a brackish layer in the same way as fish in standard cages.

4.2. Behavior modification

As implemented in previous trials, behavior modification is a low risk, low reward prevention strategy. Although cages using behavior modification trended toward reduced louse infestations, the continuous use of submerged lights and feeding did not significantly reduce louse prevalence relative to control cages (Fig. 1). There are two important factors which may have contributed to the lack of observed effect, (i) insufficient data, and (ii) sub-optimal implementation. Few trials have tested behavior modification as a louse prevention strategy in isolation, resulting in a total of only 27 available comparisons. Further subdividing those observations among salinity and temperature variables resulted in only a handful of observations in each environmental combination and subsequently limited statistical power.

Even so, it is also likely that the implementation strategy of continuously using submerged lights and feeding to lure the fish away from the surface as much as possible is sub-optimal. Given the role of salinity and temperature in determining copepodid and salmon distributions, an optimal behavior modification strategy must incorporate and respond to environmental conditions. Most important is to ensure that salmon are not being lured to cross or spend time in the halocline where infective louse copepodids aggregate. Future trials could test the following- if there is no brackish layer, lure the fish deep with submerged lights and feeding regardless of temperature. Attract the fish away from the surface as much as possible. However, if there is a brackish layer, lure the fish away from the halocline. If the preferred temperature of the salmon is in the surface, feed and position lights in the surface to attract the fish into the brackish layer. If the preferred temperature of the salmon is deep, feed several meters below the halocline to maximize growth but minimize copepodid encounters.

Although work is needed to test an environmentally responsive behavior modification strategy such as the one outlined above, the limited available data suggest that with optimization this could be a simple, low cost and low risk strategy to reduce louse infestations on commercial farms without negatively impacting growth or gill health.

4.3. Skirt barrier with behavior modification

Although skirt barriers alone are widely used in the salmon aquaculture industry, little published data examining efficacy exists (Jónsdóttir et al., 2022). As a result, these analyses focus on the combined use of skirt barriers with behavior modification (skirt+). Although the skirt+ strategy rarely achieves the 90% reduction in louse infestations possible with snorkels, the combined tools consistently cut louse infestations by 50% across all measured salinity and temperature conditions without negative impacts on growth or gill health (Figs. 1–3).

One of the most common concerns regarding barrier strategies is their purported propensity to exacerbate gill health problems. Although no data are published demonstrating such a phenomenon, extrapolation from the snorkel barrier analyses herein does support the idea that barriers increase risk of gill problems (Fig. 3). However, despite the expectation that skirt barriers would have similar effect, AGD severity in the skirt+ cages was no worse than in control cages.

Importantly, the skirt+ grouping in these analyses consists of trials using the same equipment, but according to two distinct strategies: (a) static, and (b) dynamic. While the static strategy continuously used a skirt barrier with submerged lights and feeding (Bui et al., 2020), the dynamic strategy adapted in response to real-time salinity measurements on site (Oldham et al., 2022). When salinity was homogenous throughout the water column cages were equipped with skirt barriers, aeration and submerged lights and feeding. However, when there was a brackish layer (≤ 26 ppt @ 5 m) the skirt was removed and feeding and lights were positioned at the surface to attract the salmon into the brackish layer. Thus, in contrast to snorkel cages where continuous aeration destroys the brackish layer within the snorkel, the dynamic skirt+ strategy actively encourages salmon to self-treat against AGD by attracting them into the brackish layer where there are both fewer copepodids and amoebae (Wright et al., 2017b; Crosbie et al., 2019). Subsequently, of the strategies examined, skirt+ is the safest and most effective choice for most farms.

4.4. Strategic tool choice

No single prevention strategy is the ideal for all sites. Instead, the optimal strategy must be chosen based on the needs and conditions at each location. Where louse pressure is high and fish in unprotected cages have historically required multiple delousing events in each production cycle, the increased protection from lice provided by snorkel barriers may outweigh the approximate 10% reduction in growth, particularly if AGD is rarely a concern. Indeed, Walde et al. (2022) estimated that the short-term biomass loss as a result of non-medicinal delousing was 31,200 kg from a single commercial cage stocked with 150,000 × 3 kg salmon. In such situations, where lice are the primary challenge, potential users should then consider the frequency and strength of stratification at the site. In locations with minimal freshwater input and rare haloclines, a snorkel barrier could be the optimal solution.

However, at sites where gill issues are a recurring problem or haloclines are common, snorkel barriers are not an ideal choice. Instead implementing a dynamic, environmentally responsive use of skirt barriers and adjustable depth feeding and lights would provide the most benefit – reducing louse infestations with minimal risk to fish production performance or welfare (Oldham et al., 2022).

More intensive prevention strategies than those considered in these analyses are also in development which could be integrated into planning decisions (Chu et al., 2020). Completely submerging cages can force the fish to remain well below the depths where lice and storms are a concern, but buoyancy regulation problems and exposure to poor environmental conditions during long-term submergence consistently challenged fish growth and welfare in previous trials (Sievers et al., 2022). Similarly, semi-closed and closed containment systems have also yielded promising early results, but so far have not been tested in use throughout a full production cycle (Nilsen et al., 2017, 2020; Balseiro et al., 2018; Ovrebø et al., 2022). Thus, while neither submergence nor closed containment may be the optimal single solution, each could play a role in an integrated management strategy. Closed-containment may be an ideal strategy to give smolts a strong start during sea-transfer, after which they are grown-out in cages using a dynamic skirt+ strategy (Ovrebø et al., 2022; Oldham et al., 2022). Alternatively, the skirt+ strategy could be integrated with a submersible cage such that during periods of bad weather or high louse pressure the cage would be submerged briefly but otherwise the dynamic skirt+ strategy would be utilized. In this way the negative consequences of long-term submergence for fish growth and welfare could be avoided, while louse prevention is optimized.

4.5. Future-proof farming

Salmon lice are highly adaptive and evolve rapidly in response to selective pressure (Myhre Jensen et al., 2020). As each new chemical delousing treatment was introduced, lice evolved resistance (Fjørtoft et al., 2021). Similar adaptive potential can be expected toward non-medicinal delousing methods (Ljungfeldt et al., 2017; Groner et al., 2019), and potentially preventive methods if not utilized in a considered manner (Coates et al., 2021a, 2021b). By shifting to a prevention-first lice management strategy the salmon industry could dramatically reduce the number of delousing treatments required each year, extending the functional lifespan of currently available control methods. Further, by primarily utilizing dynamic, environmentally responsive prevention strategies targeted to local conditions, the selective strength in any single direction (ie: deeper swimming, low salinity tolerance) would be minimized because tool use throughout each production cycle would vary both within and between farms.

4.6. Knowledge gaps

These analyses highlighted several key areas in need of further investigation. Although previous trials of static behavior modification alone did not significantly reduce louse numbers, optimization of the strategy to take into consideration environmental conditions and the behavioral responses of lice and salmon could improve efficacy. Given the simplicity and non-invasive nature of behavior modification as a louse prevention strategy, if optimized it could be a valuable tool in situations where more challenging options are not a possibility, such as when fish have co-morbidities that preclude the use of barriers or delousing treatments.

Also, given the promise and broad applicability of the skirt+ strategy, additional testing at sites with varying degrees of exposure and hydrographic conditions is needed to optimize the strategy for different conditions. So far data on the skirt+ strategy originate from two relatively protected fjord sites in southern Norway (Bui et al., 2020; Oldham et al., 2022). How do increased exposure or differing degrees of freshwater input impact efficacy?

Additionally, although the most data are available on snorkel barriers, many unanswered questions remain. The two key limitations to snorkel use are the increased susceptibility to AGD and deformation as a result of sensitivity to variations in water density. A possible remedy which could improve both concerns is addition of freshwater within the snorkel barrier (Wright et al., 2017a, 2018). Also unexplored is how to determine the optimal depth for snorkel barriers based on local conditions, and what the stratification intensity thresholds are for deformation with different barrier depths and aeration flow rates.

Finally, biological louse control using cleanerfish is widespread throughout the salmon aquaculture industry (Barrett et al., 2020b). However, given the sensitivity of cleanerfish to reduced dissolved oxygen levels and susceptibility to AGD (Karlsbakk et al., 2013; Haugland et al., 2017; Hvas and Oppedal, 2019; Sommerset et al., 2021), it is unclear how the use of louse prevention tools will affect cleanerfish performance and welfare. The one study which has examined the use of cleaner fishes in cages equipped with preventive tools found that wrasse in cages utilizing a skirt barrier consumed just 11% of the lice eaten by wrasse in cages without skirts (Gentry et al., 2020). Further testing is needed to determine whether or not cleanerfish can be included in integrated louse management strategies which use barrier or behavior modification tools, and if so, which species.

5. Conclusions

There are three key standards expected of an ideal salmon louse prevention strategy: (i) reduce louse infestations, (ii) not reduce growth and (iii) not negatively impact fish health or welfare. These results show that knowledge of local environmental conditions is critical for designing, selecting and deploying louse prevention tools. Adaptable to most sites, the combined use of a skirt barrier with adjustable depth lights and feeding can consistently reduce louse infestations by 50% in varied salinity and temperature conditions with no negative impacts on growth or gill health. Snorkel barriers have the potential to reduce louse infestations even more but are sensitive to salinity and temperature variability and may compromise growth and gill health. Static use of submerged feeding and lights did not, on its own, significantly reduce louse infestations, but also has obvious room for strategic optimization in relation to local salinity and temperature. Although reality is rarely ideal, with knowledge of the local environmental conditions each of the louse prevention strategies examined herein could contribute to effective louse management. In Norway, >99% of adult female salmon lice are on farmed salmonids (Dempster et al., 2021). Reducing lice on farmed fish by 50% would directly translate to reducing the louse population by 50%, and the prevention strategies exist to make this happen.

CRediT authorship contribution statement

Tina Oldham: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Data availability

Data will be made available on request.

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