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Declining size-at-harvest in Norwegian salmon aquaculture: Lice, disease, and the role of stunboats

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ABSTRACT

Sea cages used for fish farming are typically open to the environment, making the grow-out phase a race against the accumulation of infections. In Norway, farmed Atlantic salmon (*Salmo salar*) suffer outbreaks of salmon lice (*Lepeophtheirus salmonis*), which by law must be managed, and comorbid infections that weaken salmon and increase the risk of mortality following delousing treatments. To understand the role of louse management on size-at-harvest, we analysed monthly data from 1054 salmon farms over a 10-year period. Mean weight at harvest declined 6.6% (−310 g) from 2012 to 2021, with the smallest size-at-harvest occurring in months when delousing treatments were reported. In 2021, size-at-harvest was 3.4% smaller during treatment vs. non-treatment months. There is a pattern of increasing responsiveness to louse outbreaks over time, with delousing treatments preferred for small fish and harvesting preferred for large fish. There are also several lines of evidence suggesting that potential post-treatment mortalities are sometimes diverted to harvest statistics. Treatments tend to lead to higher relative mortality in the following month, except when a harvest was also reported during the treatment month. Stunboats are harvesting vessels equipped with stunning, bleeding and chilling systems, and anecdotally, are preferred for ‘emergency’ harvests. We found that stunboat visits were disproportionately associated with harvests of small fish during 2018–2021. Moreover, stunboats often visited during treatment months without any harvest being reported, consistent with accounts of stunboats standing by during risky operations to salvage moribund fish if necessary. Because harvests and mortalities are reported monthly, it is not clear how often harvests during treatment months reflect (i) harvesting of vulnerable fish as an alternative to treating, or (ii) risky treatments that produce moribund fish. However, if the latter is common, mortality statistics will underestimate the health and welfare risks of delousing treatments.

1. Introduction

Marine finfish farming in sea cages is highly vulnerable to disease outbreaks, and marine pathogens are often characterised by high connectivity over large spatial scales (Cantrell et al., 2020; Samsing et al., 2017). Transmission between neighbouring farms may be further enhanced if wild hosts act as reservoirs or vectors, and typical farm designs that rely on mesh sea cages provide little barrier to entry by pathogens (Johansen et al., 2011). One of the most severe and well-documented cases relates to ectoparasitic copepods in Atlantic salmon (*Salmo salar*) aquaculture, especially the salmon louse (Caligidae: *L. salmonis*). Severe infestations on farmed salmon have negative welfare impacts (Stien et al., 2013) and amplify infestation pressure on wild salmonids (Dempster et al., 2021; Kristoffersen et al., 2018; Taranger et al., 2015; Torrissen et al., 2013), yet a combination of high connectivity and a reservoir of wild hosts rules out eradication. Instead, farmers implement a range of measures to suppress louse densities on their fish and allow grow-out to continue (Noble et al., 2018), yielding infestation densities that exhibit seasonal cycles but are relatively stable over inter-annual timescales (Fig. 1A-B).

Medicinal treatments (chemotherapeutants) were ubiquitous through the 2000s and early 2010s, providing farmers with a highly effective and relatively gentle method of removing lice (Overton et al., 2019). However, the evolution of lice with resistance to medicinal treatments eventually forced farmers to find alternative methods (Aaen et al., 2015; Coates et al., 2021), and during 2016 onwards, the industry largely shifted from medicinal treatments to thermal and mechanical methods (Fig. 1C). These new methods are more stressful and injurious

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to treated salmon (Moltumyr et al., 2022; Overton et al., 2019; Persson et al., 2021; Sviland Walde et al., 2021), and are also less effective against early (attached) louse stages, necessitating more frequent treatment (Grøntvedt et al., 2015; Roth, 2016). This technological transition has occurred within a context of tight regulations, including the legislation of maximum allowable adult female louse densities (Ministry of Trade and Industry, 2012) and biomass caps applied to 13 spatial management zones or 'production zones' that are intended to limit the impact of farm-derived lice on wild salmonids (Ministry of Trade and Industry, 2017a). This situation, in which farmers are obliged to maintain lice at low levels using risky delousing methods, has led to a conflict between the immediate welfare of salmon and the need to reduce infestation pressure on farmed and wild salmon (Kragesteen et al., 2019; Stien et al., 2020).

The need to remain within regulatory limits while applying the fewest possible treatments (Stien et al., 2020) has led farmers to search for solutions and work-arounds, including (i) applying and reporting treatments on a cage-by-cage basis, allowing farmers to focus on the worst cages and delay treatment of fish that are close to harvest size or assessed as too weak to treat (Fig. 1D), (ii) widespread stocking of cleaner fish into sea cages in an attempt to continuously suppress densities of adult lice (Fig. 1E), and more recently, (iii) the use of preventative methods such as skirts or snorkels to reduce infestation pressure (Barrett et al., 2020; Geitung et al., 2019; Stien et al., 2018).

If the farmed cohort is close to the planned harvest date, farmers may elect to harvest early instead of treat. However, harvesting is only expected to be preferred if the opportunity cost of lost future growth is less than the cost of delousing. The cost of delousing includes service fees and labour (which together, can be upwards of 100,000 USD per day: (Iversen et al., 2020, Iversen et al., 2015), but also lost or foregone production, which occurs because fish are usually fasted prior to treatment, may not feed for some time afterward, and can be injured or killed by the treatment (Moltumyr et al., 2022). Treatment-related mortality, which often accumulates over the days or weeks following the treatment, is believed to be more common when the fish have comorbidities such as pancreas disease, cardiomyopathy syndrome or amoebic gill disease (Oliveira et al., 2021; Sviland Walde et al., 2021). If moribund fish cannot be harvested before they die, all costs that have been invested in rearing them become a total financial loss for the farmer. Essentially, the decision to delouse or harvest is a cost- or risk-optimisation problem, which takes place within limits set by regulators, the needs of the company and fish welfare (Stien et al., 2020; Størkersen et al., 2021).

Decisions to delouse or harvest may also be influenced by local availability of specific infrastructure and services. One such case is the recent development of harvesting vessels with on-board slaughtering capabilities (first used in 2006 in Canada and 2008 in Norway: (Oaland, 2019). These vessels have been variously termed 'stunboats', 'stun-and-

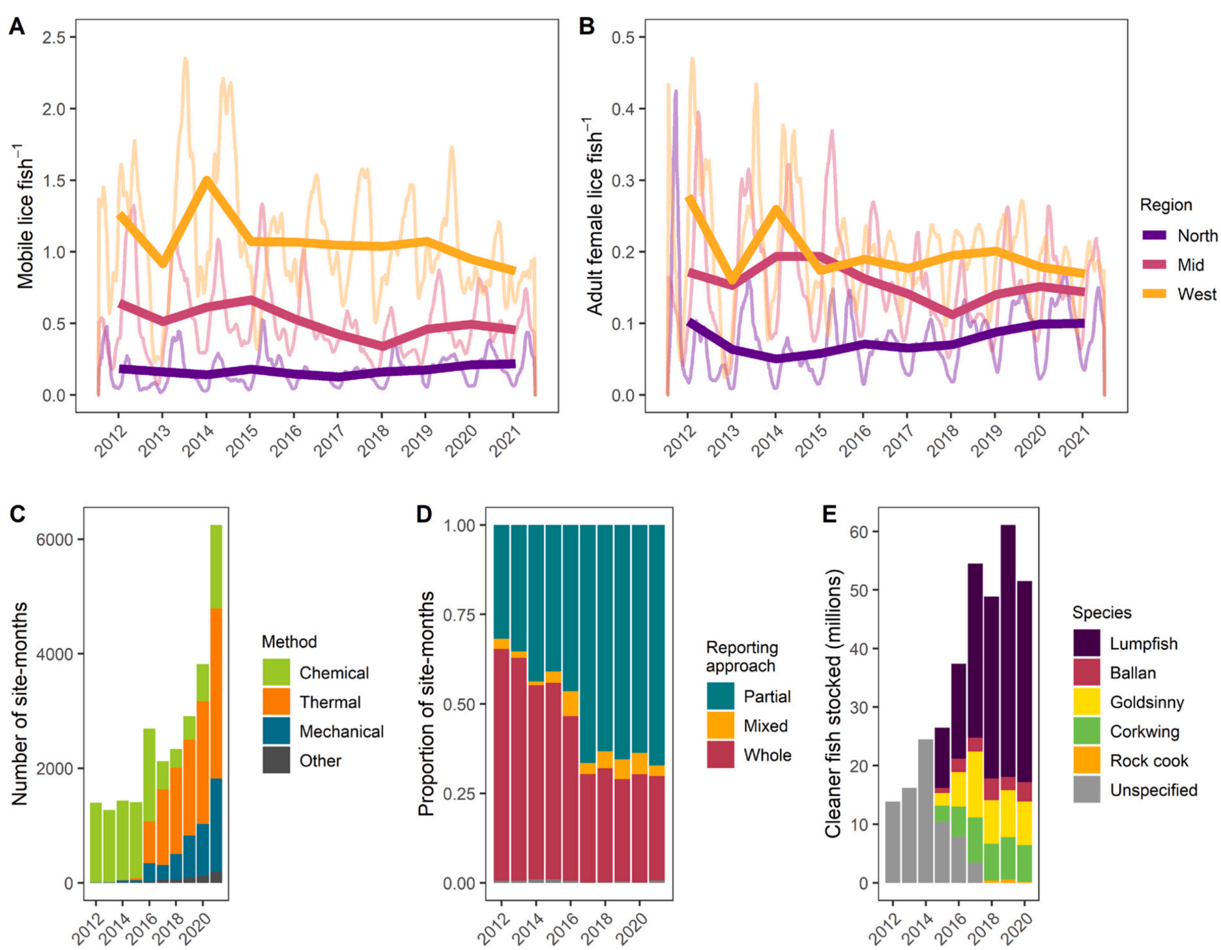

Fig. 1. Long-term patterns in salmon louse infestation density and control strategies (bottom row) in Norway during 2012–2021. The upper row shows that mean infestation densities of all mobile lice (A) and adult female lice only (B) have remained relatively stable year-to-year, but with reduced seasonal variability in recent years. Thin lines show the 6-week moving average with weekly resolution; thick lines show annual means by region. The lower row shows that: (C) preferred treatment methods have changed over time, particularly between 2015 and 2016; (D) reporting approaches shifted around the same time, from whole farm reporting, usually with zero or one report per month, to partial farm reporting, sometimes with multiple reports per reporting period; (E) use of cleaner fish has increased over time (data were available for 2012–2020 only).

bleed boats', 'processboats' and 'processing boats', with the core feature being the presence of equipment to stun, bleed and then chill the salmon. Cage-side slaughter has numerous potential advantages compared to transport of live fish to onshore slaughterhouses, including (i) improved animal welfare, as fish do not experience multiple transfers and a long journey in a vessel's hold, (ii) improved biosecurity, as live fish are not transported long distances to a slaughter house but instead killed on-site with requirements to disinfect wastewater and the vessel before the next assignment), (iii) improved efficiency, as smaller vessels can be used for the same harvest volume, and (iv) avoidance of the wastage that occurs when weak fish die during transport and must be discarded (Midling et al., 2011; Ringvall, 2020). A questionnaire given to salmon farmers by the Norwegian Veterinary Institute in 2020 indicated that 31 out of 70 respondents had been involved with delousing operations using stunboats on stand-by in case of moribund fish (18% answered "often" or "very often": (Sommerset et al., 2021)). In the same report, it was noted that while stunboats can improve welfare outcomes for farmed salmon, the capacity to salvage moribund fish could also increase willingness to perform risky delousing operations. Thus, the role of stunboats in treatment vs. harvest decisions, and the animal welfare implications of those decisions, warrant investigation.

Here, we show that size-at-harvest has declined between 2012 and 2021, and (1) investigate whether the decline is related to the pressures of salmon louse and other disease control management; (2) test whether responses of farmers to salmon louse outbreaks have changed over time; (3) document the spatial distribution of farm visits by stunboats in Norway, and describe the likely role of these vessels based on reported treatments and harvests coinciding with visits by stunboats; (4) model farm-scale decisions to delouse or harvest according to the size of the fish and presence of disease; and (5) assess evidence that impending post-treatment mortality is frequently avoided by emergency harvests during treatment months, especially through the use of stunboats.

2. Methods

2.1. Data sourcing and initial cleaning

Norwegian regulations on the operation of aquaculture production sites require fish farming sites to report various data weekly to the Norwegian Food Safety Authority and monthly to the Directorate of Fisheries (Ministry of Trade and Industry, 2008, 2012). To document patterns of delousing and harvesting, we combined data from both sources.

2.1.1. Harvest and mortality data (Directorate of Fisheries)

Monthly reports to the Directorate of Fisheries include cage-level data on fish year-class, number of fish, mortalities, and the number and weight of fish harvested or transferred. Data reported to the Directorate of Fisheries are confidential and any users granted access must abide by strict data privacy rules. The data were initially cleaned by omitting reports relating to rainbow trout, omitting harvest reports of less than 100 kg or 10 individual salmon.

2.1.2. Louse density, delousing treatment, disease (Food Safety Authority)

Weekly reports to the Food Safety Authority include site-level data on sea temperature, mean number of salmon lice (*L. salmonis*) per fish (categorised as sessile, mobile or adult female stages), and any delousing treatments along with the date, method and any specific substances used. Quantities and species of cleaner fish stocked for louse control were reported to the Food Safety Authority until responsibility was transferred to the Directorate of Fisheries in 2018–2019. Cases of pancreas disease and infectious salmon anaemia are also recorded. We downloaded files containing louse counts, treatment reports and disease status for all sites from 2012 to 2021. Louse density reports undergo an initial cleaning process at the Food Safety Authority, and we assumed all reported densities to be correct - it is not possible to reliably detect errors where plausible numbers have been reported. Delousing reports were cleaned by consolidating variations in the spelling or naming of common delousing methods, and categorising those methods into 5 categories: Thermal, Mechanical, Bath, In-feed, and Other. Thermal methods were identified by mention of Thermolicer or Optilicer systems, as well as generic terms such as "warm water" (in Norwegian). Mechanical treatments were identified by mention of Hydrolicer, SkaMik, Optilicer or Flatsetsund/FLS systems, as well as generic terms such as "flush". Bath and in-feed treatments were generally clearly reported as such. Occasional misspellings or other variations were manually recoded if the correct coding was obvious. Remaining reports with unclear methods or substances were placed within the 'Other' category. Treatment reports typically stated a start and end date. Where this was not stated, we assumed that the report date was the sole treatment day.

2.1.3. Vessel visits (BarentsWatch)

The BarentsWatch fish health application (https://www.barentswatch.no/) uses nonconfidential data from the Directory of Fisheries and Norwegian Food Authorities databases to provide up-to-date data on lice and lice treatments at all Norwegian aquaculture sites. BarentsWatch also uses other data sources, including automatic identification system (AIS) data on movements and farm site visits by AIS-enabled vessels. The AIS data can be viewed directly on the website or downloaded through an application programming interface (API). We used the API to obtain a list of the names and identification numbers of all tracked vessels, together with their International Maritime Organisation designation (e.g. wellboat, small workboat, fishing vessel). We then used a variety of sources, including company websites, news articles and images to manually corroborate or update the designation and purpose of each vessel, particularly whether it possesses onboard stunning, bleeding and chilling capabilities. Among those vessels, we excluded fish factories (e.g. Norwegian Gannet) and vessels for which harvesting was a secondary role (e.g. the delousing vessel Gåso Freja), ultimately yielding a list of 14 stunboats. This list is not exhaustive, but each vessel is included with high confidence. For each stunboat on the list, we then obtained a record of all probable farm site visits during 2018–2021. For older vessels that were refitted with stun-and-bleed facilities during 2018 or later, we omitted any visits that occurred prior to the refit.

2.2. Data aggregation and additional cleaning

The various datasets were aggregated and joined as necessary to address specific research questions. In each case, the temporal resolution was limited by the dataset with the lowest resolution (harvests and mortalities are reported monthly, louse density weekly, delousing daily, and vessel visits in real-time). This means that, for example, all analyses involving harvest or mortality data are limited to monthly time-steps. Due to difficulties in reliably tracking cage-level data (when available) through time, all data were aggregated to the level of farm sites (also called localities). We use the term 'site-months' to denote monthly time-steps with site-level data.

Before fitting any models, we omitted all records for sites with licenses for slaughter holding pens, broodstock or research, as of Nov 2021, as these facilities may not be representative of typical commercial grow-out sites. We also omitted site-months with suspected or confirmed infectious salmon anaemia virus, as the Norwegian Food Safety Authority enacts temporary local regulations to limit further spread of the virus when detected, often including a requirement to slaughter the fish.

For analyses of mortality rates, cage-level fish movement reports were aggregated to site level by summing end-of-month fish counts (*end*), additions (*in*) and all removal categories (*out*). Based on these values, we back-calculated fish counts at the start of the month: $start = end + out - in$. In rare cases (<0.3% of site-months), this calculation yielded a negative value for *start*, indicating data entry errors, and affected site-months were omitted.

The final dataset included 1054 sites and 83,168 site-months (median 75 months per site).

2.3. Analysis

We specified 4 main models (Models 1–4) corresponding to 4 research questions regarding long-term patterns in size-at-harvest (with small sizes assumed to indicate early harvests), responsiveness of farmers to louse outbreaks, decisions to delouse or harvest, and the association between post-treatment mortality and emergency harvests. We fitted several versions of each model to test multiple hypotheses relating to the same research question. All variables used in model fitting are described in Table 1, while model specifications are given in Table 2.

It is important to consider the role of comorbidity in decisions to delouse or harvest. The only comorbidities with routine status reporting by farmers are infectious salmon anaemia (ISA), caused by the infectious salmon anaemia virus, and pancreas disease (PD), caused by salmon alphavirus. As site-months with infectious salmon anaemia are omitted, PD is the only remaining comorbidity that can be accounted for within this analysis. We do this by including a variable for PD status in each model and adjusting model predictions for PD status.

2.3.1. Model 1: Long-term patterns in size-at-harvest

To test whether salmon lice and associated requirements are correlated with early harvests, we fitted a generalised additive model (GAM) to monthly site-level size-at-harvest data spanning 2012–2021. The model was fitted using the *gam* function in the mgcv package for R (Pedersen et al., 2019; R Core Team, 2020; Wood, 2011) with a Gaussian model family. To detect differences in size-at-harvest (W_{Hit}) during site-months with or without delousing treatments, the model included time (t) and treatment status (T_{it}) effects. Time was fitted as a smooth term within levels of treatment status, using a shared smoother of the factor smooth type (bs = "fs") (Pedersen et al., 2019). The basis complexity (k = 45) and penalty (m = 1) were selected to give the model freedom to follow seasonal patterns in size-at-harvest over the 10-year timeframe. To minimise model complexity while accounting for latitudinal or other regional effects, we fitted 3 datasets individually, each containing records from western (Model 1A), mid (Model 1B), or northern Norway (Model 1C), respectively. These regions were defined according to regulatory production zones (west: 2–5; mid: 6–10; north: 11–13) (Ministry of Trade and Industry, 2017a). Model fits were assessed using the *gam.check* function in mgcv. Model predictions and confidence intervals were extracted using the *predict_gam* function in the tidymv package (Coretta, 2021), and plotted using the ggplot2 package (Wickham, 2016).

2.3.2. Model 2: Responsiveness to louse outbreaks

To test whether salmon farmers in Norway are becoming more responsive to salmon louse outbreaks, we first limited the dataset to site-months in 2012–2020 with high louse levels, defined as cases in which the adult female louse density in the previous month (L_{it-1}) was >75% of the maximum allowable density for the month. The allowable density was normally 0.5 adult female lice fish^{-1}, or else 0.2 during the spring salmon outmigration season. We then fitted three related models to response variables indicating whether the site had treated (T_{it}, Model 2A), harvested (H_{it}, Model 2B), or taken either action (A_{it}, Model 2C) during the month in question. We used a generalised linear mixed effects modelling (GLMM) approach, specified with a binomial family and logistic link function. The three models were each specified with terms for time (t), PD (P_{it}) and region (R_i), including a $t \times R_{it}$ interaction term. We also specified a random intercept term for farm site identity (i) to account for any consistent differences in the responsiveness of individual farms through time. These and all other GLMMs were fitted using the *glmmTMB* function in the glmmTMB package for R (Brooks et al., 2017). Model fit was assessed using the *simulateResiduals* function in the DHARMa package (Hartig, 2019), and analysis of deviance tables (type II Wald X^2) were generated using the *Anova* function in the car package (Fox and Weisberg, 2019). Predictions and confidence intervals were

Table 1
List and description of all variables.

Notation	Name	Description
i	Site	Unique identifier for the farm site (also known as a locality)
Z_i	Production zone	The legislated production zone containing site i (there are 13 zones, designated 1 to 13 from south to north)
R_i	Region	The region within which site i is located, coded as a factor with 3 levels defined according to regulatory production zones (West = zones 2–5, Mid = zones 6–10, North = zones 11–13). Zone 1 is omitted from the entire analysis, as this zone has few farms and fish health challenges that are distinct from the rest of the country, including relatively few salmon lice. Analyses of mortality and stunboat visitation only consider data from zones 2–8
t	Time	Monthly time steps (integer)
Y	Year	Annual time steps (integer)
W_{Hit}	Size-at-harvest	Mean size-at-harvest, i.e. slaughter weight, of fish that were harvested at site i during month t (numeric, kg). Reported at cage-level and aggregated to site-level via a weighted mean (values weighted by the mean number of fish in each cage during month t)
W_{Eit}	Mean size (estimated)	Estimated mean size of all fish at site i during month t (numeric, kg). Reported at cage-level and aggregated to site-level via a weighted mean (as for W_{Hit})
W_{it}	Mean size (overall)	Overall site-level mean size of fish at site i during month t. If only W_{Hit} is reported, $W_{it} = W_{Hit}$; if only W_{Eit} is reported, $W_{it} = W_{Eit}$; if both are reported, W_{it} is the mean of both
T_{it}	Treated	Binary factor indicating whether site i has reported any delousing treatments during month t. In-feed medicinal treatments were not considered. A 1-month time-lagged variable was also used: T_{it-1}
P_{it}	Pancreas disease	Binary factor indicating presence or absence of pancreas disease at site i during month t (no distinction between suspected or confirmed cases, nor SAV2 and SAV3 strains)
A_{it}	Some action taken	Binary factor indicating whether site i had taken any action (harvesting and/or treating) during month t
L_{it-1}	Louse density	Mean density of adult female salmon lice (numeric, fish^{-1}) reported by site i during the previous month $t-1$. Lice are reported weekly, and aggregated to months
$\widehat{L}_{it-1}$	Proximity to louse limit	Ratio variable indicating the louse density in the previous month relative to the allowable limit for the previous month: $\widehat{L}_{it-1} = L_{it-1}/K_{it-1}$ where K_{it-1} is the maximum allowable louse density for the previous month
V_{it}	Visited	Binary factor indicating whether site i was visited by a stunboat during month t
N_{it}	N fish	Estimated mean number of fish at site i over month t, obtained by aggregated cage-level reports to site-level: $N_{it} = \sum b_c - \left(\frac{w_c}{2}\right) \Big/ \left(\frac{a_c}{2}\right)$ where b_c is the number of fish in the cth cage at the start of the month, w_c is the number of fish withdrawn from the cage for any reason during the same month, and a_c is the number of fish added to the cage during the same month
N_{Hit}	N harvested	Number of fish harvested by site i during month t
N_{Mit}	N mortalities	Number of fish reported as mortalities by site i during month t
$\widehat{M}_{it}$	Mortality rate	Ratio variable indicating the mortality rate of fish at site i during month t: $\widehat{M}_{it} = N_{Mit}/N_{it}$
H_{it}	Harvested	Binary factor indicating whether site i harvested any volume of fish during month t. Time-lagged and time-led variables were also used: H_{it-1} and H_{it+1}
$\widehat{H}_{it}$	Harvest rate	Ratio variable indicating the harvest rate of fish at site i during month t: $\widehat{H}_{it} = N_{Hit}/N_{it}$
$\widehat{M}^{\sigma}_{it}$	Relative mortality	Relative monthly mortality for site i and a 3-month window of time centred on month t, expressed as the log rate ratio of mortality in the following month $t+1$ relative to the previous month $t-1$: $\widehat{M}^{\sigma}_{it} =$

(*continued on next page*)

Table 1 (*continued*)

Notation	Name	Description
		$ln\left(\frac{\widehat{M}_{it+1}}{\widehat{M}_{it-1}}\right)$. Values of 0 or 1 for $\widehat{M}_{it}$ or $\widehat{M}_{it-1}$ were adjusted to 0.0001 or 0.9999 before computing $\widehat{M}_{it}^{\sigma}$

Table 2
Model specifications.

Model	Type	Outcome	Model terms	Model family
1A	GAM	Size-at-harvest	$W_{Hit} \sim s(t, by = T_{ij})$	Gaussian
1B	GAM	Size-at-harvest	$W_{Hit} \sim s(t, by = T_{ij})$	Gaussian
1C	GAM	Size-at-harvest	$W_{Hit} \sim s(t, by = T_{ij})$	Gaussian
2A	GLMM	Treatment conducted	$T_{ij} \sim t * R_i + P_{it} + (1\|i)$	Binomial (logistic link)
2B	GLMM	Harvest conducted	$H_{ij} \sim t * R_i + P_{it} + (1\|i)$	Binomial (logistic link)
2C	GLMM	Either conducted	$A_{ij} \sim t * R_i + P_{it} + (1\|i)$	Binomial (logistic link)
3A	GLMM	Treatment conducted	$T_{ij} \sim W_{it} * V_{it} * \hat{L}_{it\text{-}1} * P_{it} + (1\|i)$	Binomial (logistic link)
3B	GLMM	Harvest conducted	$H_{ij} \sim W_{it} * V_{it} * \hat{L}_{it\text{-}1} * P_{it} + (1\|i)$	Binomial (logistic link)
4A	LM	Relative mortality rate	$M_{it}^{\sigma} \sim T_{it} * H_{it} * R_i + T_{it\text{-}1} + T_{it+1} + H_{it\text{-}1} + H_{it+1}$	Gaussian
4B	LM	Relative mortality rate	$M_{it}^{\sigma} \sim T_{it} * V_{it} * Y_t + T_{it\text{-}1} + T_{it+1} + H_{it\text{-}1} + H_{it+1}$	Gaussian

Refer to Table 1 for descriptions of model terms. Model formulae are given in R syntax: response ~ predictor, with asterisks denoting where interactions are included. The '*s()*' within the generalised additive model (GAM) formula denotes a smoothing term, which is fitted within levels of a grouping factor named using the '*by*' argument.

extracted using the ggeffects package (Lüdecke, 2018) and plotted using ggplot2. A similar evaluation and interpretation procedure was followed for each of the models below.

2.3.3. Model 3: Decisions to delouse or harvest during louse outbreaks

To model decisions to delouse or harvest, we fitted a binomial GLMM with a logistic link function to monthly site-level data spanning 2018–2021 in production zones 2–8 (the timeframe and zones in which stunboats were active). We omitted site-months where mean fish size was <0.25 kg, as such fish are rarely deloused or harvested. For Model 3A, the response variable was treatment status (T_{it}), predicted by model terms for mean fish size (W_{it}), lice (L_{it-1}), visitation by stunboats (V_{it}), PD status (P_{it}) and region (R_i). We also included full interactions between W_{it}, L_{it-1}, V_{it} and P_{it}. Region was removed from the final fit as it explained little variance and was not central to the hypothesis. As comorbidities such as PD could also make delousing riskier, model predictions regarding the stunboat effect are conditional on negative PD status. We also extracted predictions for the PD effect, regardless of stunboat visitation. Model 3B was specified as for Model 3A, but with harvest status (H_{it}) as the binary outcome.

2.3.4. Model 4: Do emergency harvests mask health and welfare impacts of delousing treatments?

Post-treatment mortality rates, viewed in isolation, may underestimate the health and welfare impacts of delousing treatments if affected fish are harvested before dying, leading to a mortality rate that is within the normal range. One possibility is to test whether harvests are associated with lower mortality rates relative to comparable months without harvests. However, monthly mortality rate calculations can be biased if a substantial proportion of the fish are harvested (or removed for any other reason), as the number of fish at the start of the month may be much larger than at the end of the month, leading to differing mortality rate estimates depending on which number is used as the denominator in the mortality rate calculation. Because removals and additions are only available with monthly resolution in the Directorate of Fisheries database, we calculated a hedged monthly mortality rate using the mean of the number of fish at the start and end of the month. This means that if a large harvest or mortality event occurs early or late in the month, we could substantially under- or overestimate the true mortality rate. To mitigate this issue, we tested for a correlation between harvesting and post-treatment mortality over a 3-month window (Fig. 2). We predict that harvests conducted during a treatment month t will lead, on average, to lower relative mortality in month $t + 1$ relative to month $t - 1$, based on an expectation that weak or moribund fish will have been preferentially harvested.

We fitted Model 4A with relative mortality as the response variable ($\widehat{M}_{it}^{\sigma}$), predicted by treatment status (T_{it}) and harvest status (H_{it}) during month t, as well as region (R_i), with 2-way and 3-way interactions between each of these terms also specified. The model also included main effects to control for treatment and harvest status during the previous and following month: T_{it-1}, T_{it+1}, H_{it-1} and H_{it+1}. The dataset contained site-months in production zones 2–13 during 2012–2021. Site-months with cages holding fish smaller than 0.25 kg or larger than 3.5 kg were omitted to ensure that the model represents fish that are large enough to be treated if necessary but would not be harvested under ideal circumstances.

Model 4B was specified as for Model 4A, but with stunboat visitation (V_{it}) instead of harvest status (H_{it}), and year (Y) instead of region (R_i), as there were too few site-months with stunboat visits in the mid and north regions to test for a regional effect. The dataset used for Model 4A was also filtered to 2018–2021 and production zones 2–7, as there were no stunboat visits north of zone 7 remaining once the dataset had been limited to site-months with fish between 0.5 and 3.5 kg. This resulted in a sample size of 153 site-months with stunboat visits and 5635 without. Given this small sample size and the model complexity, we consider the group means and adjusted model predictions to be unreliable in isolation, but useful as an additional line of evidence alongside the findings from Model 4A.

3. Results

Model summary tables are included as supplementary information (Models 1A-C: Tables S1–3; Models 2A-C: Tables S4–6; Models 3A-B: Tables S7–8; Models 4A-B: Tables S9–10).

A typical salmon harvested in 2021 was 310 g smaller than one harvested in 2012 (4.25 kg cf. 4.56 kg; 6.6%). These values are based on reported mean size-at-harvest per month at each site, weighted according to the number of fish harvested during each site-month, and excluding site-months with pancreas disease or infectious salmon anaemia present. There was a 6.9% decline in the median size-at-harvest, from 4.50 kg in 2012 to 4.21 kg in 2021. The decline occurred in all three regions (west, mid, north), although typical size-at-harvest differed between regions, with harvested fish tending to be smaller in the western region (weighted mean 4.19 kg in 2021). The largest decline occurred in the north, from 4.98 kg in 2012 to 4.22 kg in 2021 (18%) (Fig. 3). One possible explanation for the widespread decline is that the need to manage louse infestations is driving earlier harvest. Consistent with this hypothesis, Models 1A, 1B and 1C also indicate that fish harvested in the same month as delousing were smaller on average (in 2021, 4.14 kg cf. 4.30 kg). This relationship was statistically significant across western, mid and northern Norway ($p < 0.0001$ in each case: Tables S1-S3).

It is difficult to track the responsiveness of farmers to salmon louse outbreaks over time because preferred treatments shifted markedly between 2012 and 2021 (Fig. 1C). Likewise, methods of reporting treatment to authorities shifted from predominantly 'whole farm' reports in the early 2010s to predominantly 'partial farm' reports since 2017 (Fig. 1D). By recording binary treatment status for each site-month, we aim to reduce the influence of partial farm reports, as multiple reports

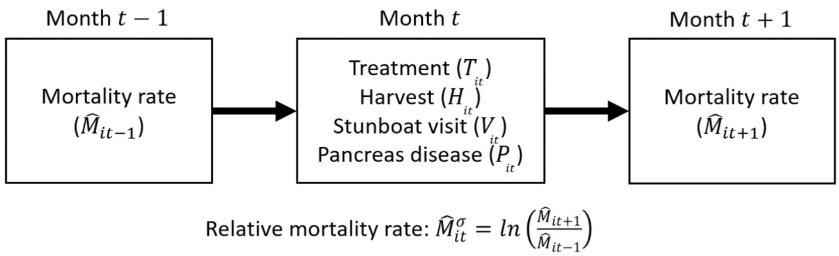

Fig. 2. Diagram of the 3-month window considered by Models 4A and 4B. Events during month t are hypothesised to affect the mortality rate during month $t+1$ (relative to the baseline mortality rate in month $t-1$).

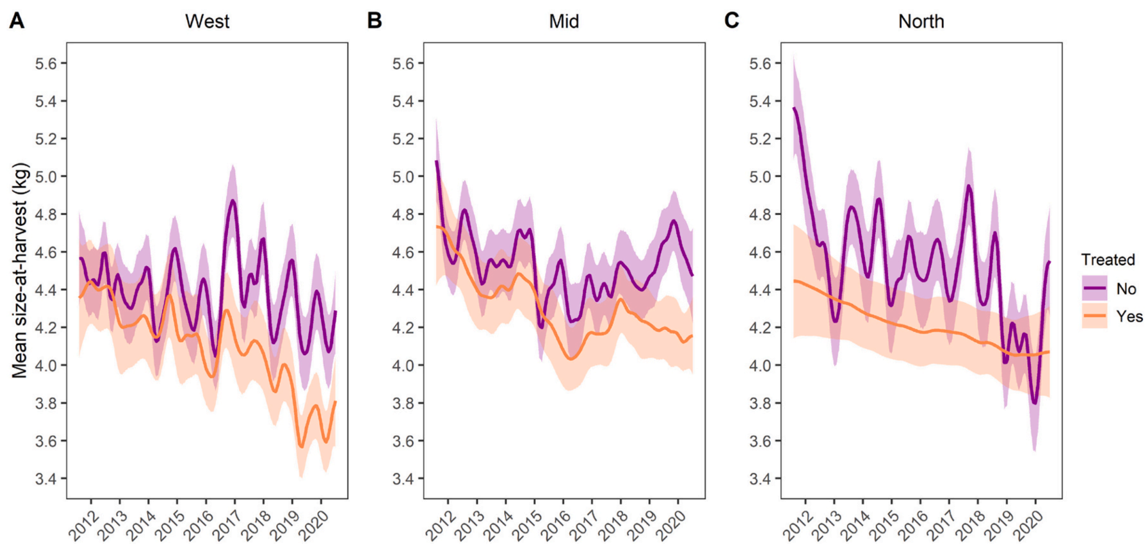

Fig. 3. Long-term patterns in salmon size-at-harvest within (A) western, (B) mid and (C) northern Norway during 2012–2020. Plots show predictions from generalised additive models fitted to a time series within each region (monthly time steps). Regions are defined according to regulatory production zones (West = zones 2–5, Mid = zones 6–10, North = zones 11–13). The models contained a temporal smooth fitted to site-level monthly harvest reports. Smooths were fitted within levels of the factor T_{it}, indicating whether a delousing treatment was reported during the same month as the harvest. Shading denotes 95% confidence intervals around the model fit.

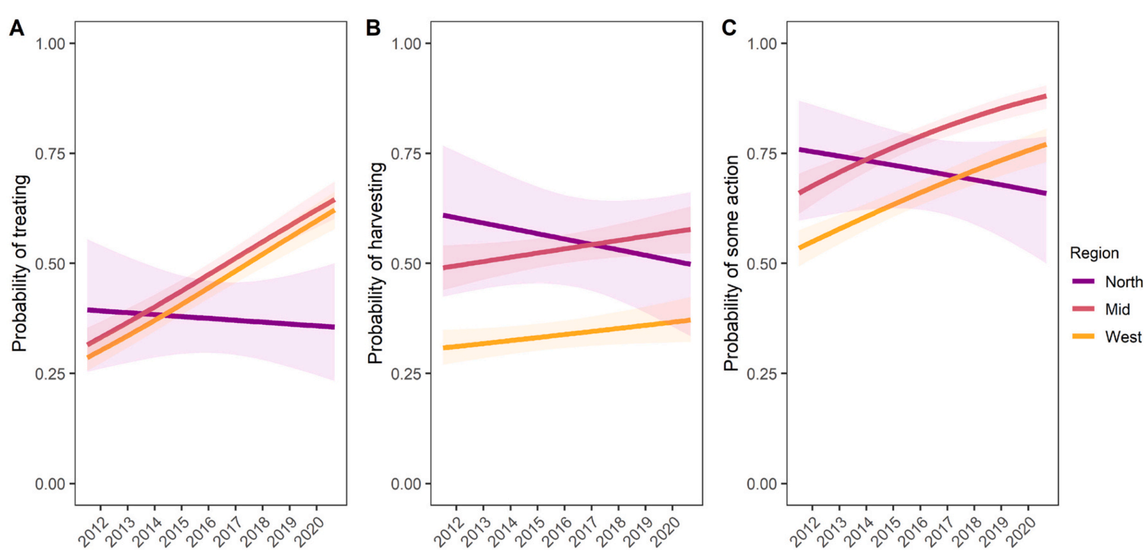

Fig. 4. Long-term changes in responsiveness to high densities of salmon lice, in terms of the probability of farmers reporting (A) a delousing treatment (T_{it}, Model 2A), (B) a harvest (H_{it}, Model 2B), or (C) either action (A_{it}, Model 2C) in the month following a report of adult female salmon louse densities exceeding 75% of the allowable limit ($\widehat{L}_{it-1} > 0.75$). Probabilities are predicted by generalised linear mixed effects models with a binomial family and logistic link function. Shaded ribbons indicate 95% confidence intervals around predictions. Predictions are conditional on an absence of pancreas disease.

within the same month—for example, where treatments are reported as they are applied to individual cages—will have the same weight as one whole-farm report. We also avoid inferring a change in the number of treatments experienced by an average farmed salmon. However, we do find evidence that between 2012 and 2021, farmers in west and mid (but not north) Norway became more responsive to high densities of adult female lice (defined as >75% of the allowable limit). Adjusted predictions from Model 2A indicated farms were twice as likely to delouse in 2021 than 2012, increasing from 30% to 65% in the west and from 33% to 67% in mid Norway (Fig. 4A; Table S4). The probability of harvesting or taking either action also increased over time, although less markedly (Fig. 4B-C; Tables S5-S6). The presence of PD was associated with a 14–16% lower probability of delousing and an 18–25% higher probability of harvesting (Tables S4-S5), although with this model specification, the effect of PD on delousing/harvesting decisions is confounded by fish size, as large fish are more likely to have PD and are also more likely to be harvested than small fish. To ensure that these findings are robust to the aforementioned changes in preferred treatments and reporting methods, we fitted the same models to a subset of the data spanning 2017–2021. The greatest changes occurred around 2016, making 2017–2021 a relatively stable period in terms of the predominant louse management strategies (Fig. 1C, E). Models 3A-C returned qualitatively similar outcomes when fitted to this shorter timeframe (Tables S11-S13).

Collectively, during the period from 2018 to 2021, the 14 tracked stunboats made numerous farm visits in production zones 2–8 (Fig. 5A). No visits were recorded in zones 9–13. During 2021, 8% of reported harvest volume in zones 2–8 occurred during site-months in which at least one stunboat visited (Fig. 5B). However, this should not be taken to mean that stunboats harvested that volume, as stunboats may visit without harvesting, or share harvesting duties with other vessels. Site visits by stunboats were usually associated with harvesting, delousing, or both during the same month (Fig. 5C). Notably, 20% of site visits during the study period coincided with delousing but no harvesting at

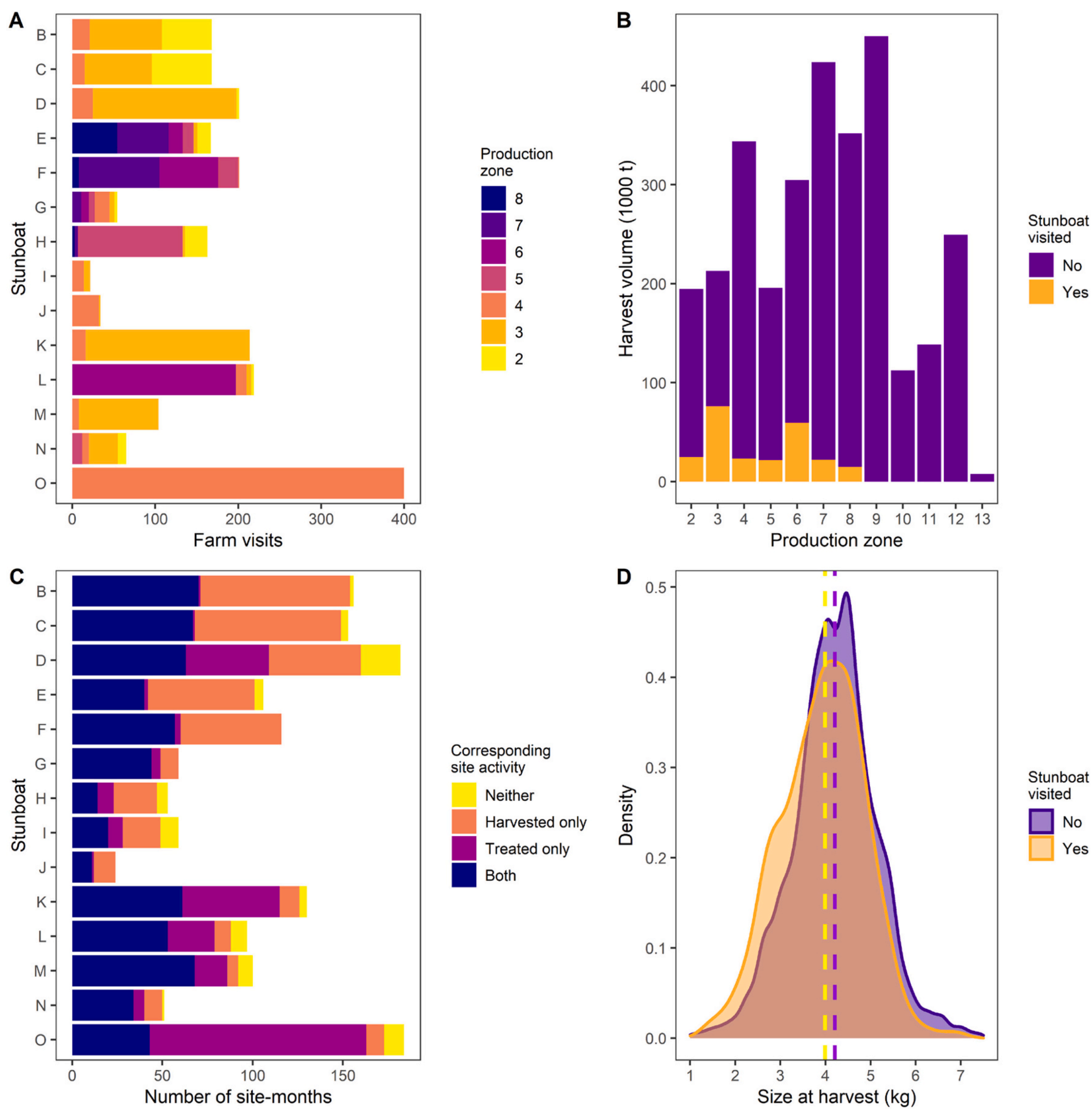

Fig. 5. Spatial distribution of Norwegian stunboats during 2018–2021, with visits aggregated to production zones. (A) The latitudinal distribution of individual stunboats in terms of the number of farm visits within each production by each stunboat. Vessels are anonymised. (B) The proportion of harvest volume in each production zone that coincided with stunboat visits during 2021. Note, the bars are overlaid, not stacked. No stunboats visits were identified north of production zone 8 during the period monitored. (C) Site activities corresponding to visits by stunboats. (D) The distribution of size-at-harvest based on whether a stunboat was present during that month or not. Dashed lines indicate the median size-at-harvest (yellow = stunboat visit, purple = no stunboat visit). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that site. There is substantial overlap in the size distribution of fish harvested during months with and without stunboat visits, yet there is some evidence that stunboats are preferred for harvests of small fish (Fig. 5D).

Given that stunboats may play a different role to other harvest vessels, it is worth considering which farm activities lead to visits by stunboats, or switching the assumed direction of causality, whether the availability of stunboats influences decisions to treat or harvest fish with heavy louse infestations. Model 3A showed that delousing treatments were significantly more likely when louse levels were high and/or fish were small (Fig. 6A; Table S7). Model 3B showed that harvest was also more likely when louse levels were high, but was less likely if the fish were small (Fig. 6B; Table S8). Stunboat visits were more likely to occur during either treatment or harvest months. Overall, responses to louse outbreaks were very likely to involve some harvesting as fish approached an ideal harvest size of ~5 kg, although treatment rates remain high throughout the size range. Notably, stunboat visits were a strong predictor for harvest of very small fish, consistent with an emergency harvest role (Fig. 6B). For example, at a site holding ~2 kg fish, a stunboat visit increases the probability of harvesting from 7% to 71%. PD status was also related to treatment and harvest decisions (Tables S7-S8), such that PD-positive fish were less likely to be treated (Fig. 6C) and more likely to be harvested (Fig. 6D) than PD-negative fish of a similar size.

Model 4A found evidence of post-treatment mortality, with higher relative mortality after treatment months than non-treatment months (Fig. 7A; Table S9). However, harvests conducted during treatment months appeared to mitigate post-treatment mortality (Fig. 7A; Table S9). Given that the model was fitted to data from cohorts that were too small to be harvested under ideal conditions (0.25–3.5 kg), this finding is suggestive of emergency harvesting of fish that either could not be treated due to comorbidities or other risk factors, or else were treated and were severely affected by the treatment. Model 4B did not find stunboat visits to be a significant predictor of mortality (Fig. 7B, Table S10), although the model was affected by low statistical power. Mortality rates are highly variable and preparing the dataset for this model resulted in a much smaller sample size than for previous models: 668 site-months with harvesting reported, of which only 188 coincided with a stunboat visit.

4. Discussion

Salmon are being harvested at a smaller size in recent years, and fish harvested during treatment months tend to be smaller. Together, these findings suggest that the observed decline in size-at-harvest is related to louse infestations or their management. We found evidence that farmers in western and mid Norway are treating more often in response to high louse levels. For fish with high louse levels, delousing is preferred when fish are small and harvest is preferred when fish are large, although the presence of a comorbidity (PD) increased the probability of small fish being harvested rather than treated. We found evidence that post-treatment mortality is reduced when harvesting takes place during treatment months. These putative emergency (early) harvests, which are related to louse management, may be a large component of the decline in mean size-at-harvest. Stunboats appear to be preferred for emergency harvests, especially when the fish are small, although probable emergency harvests regularly occur in the absence of stunboat visits.

4.1. Lice, comorbidities and size-at-harvest

There are many possible reasons for farmers to harvest their fish early. These include harvesting healthy fish early to take advantage of high spot prices (Asche et al., 2018; Forsberg and Guttormsen, 2006) or to remain within the regulatory biomass caps that are applied to specific sites, maximum allowable stocking density per cage, and biomass caps that are applied to companies within each region (Bjørndal and Tusvik, 2020; Ministry of Trade and Industry, 2008). Biomass and density caps are known in advance, and farmers can therefore optimise their production plans to avoid exceeding their allocation, usually aiming to harvest at a relatively large size if possible (>5 kg), as growth efficiency remains high throughout the cycle and large fish attract a higher per-kg price (Berge, 2021; SjømatNorge, 2020). If high mortality is expected, farmers may also over-stock at the start of a grow-out cycle to avoid falling short of the allowable biomass. If mortality is then lower than expected, it may be necessary to conduct small 'spot' harvests later in the grow-out cycle. However, farmed cohorts do not always remain free

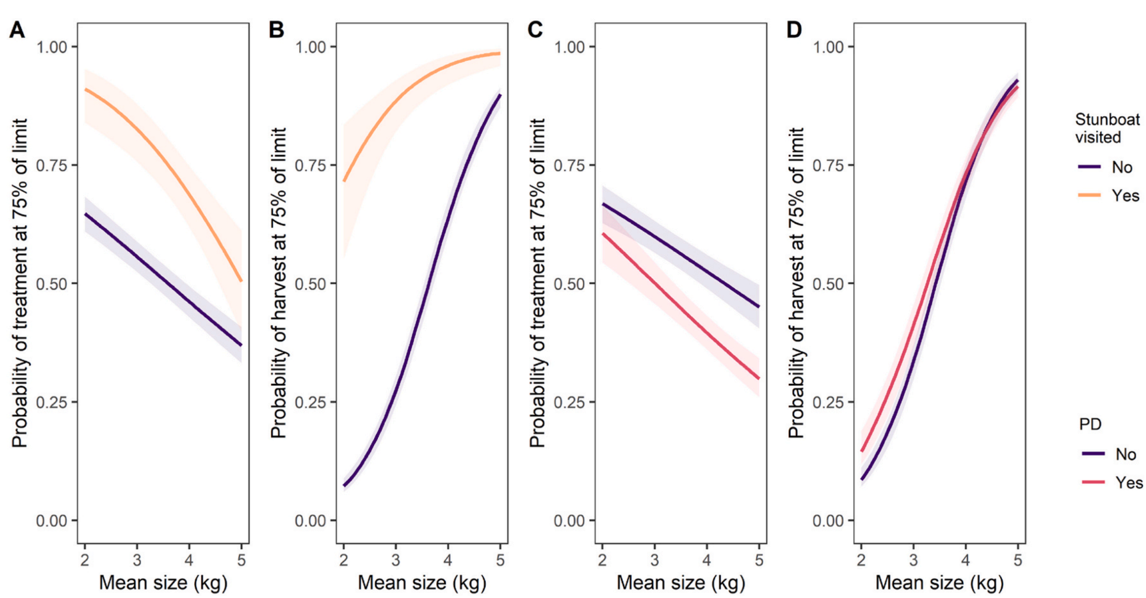

Fig. 6. Adjusted predictions from Models 4A (panels A and C) and 4B (panels B and D), indicating that given high louse levels, sites are more likely to treat small fish and harvest large fish. These decisions are also predicted by stunboat visitation (panels A and B) and pancreas disease status (panels C and D). Both models were fitted to data from 2018 to 2021 in production zones 2–8. Predictions in all panels are conditional on a reported density of adult female lice at 75% of the maximum allowable limit at the time ($\widehat{L}_{it-1} = 0.75$). Predictions in panels A and B are conditional on negative pancreas disease status; predictions in panels C and D are conditional on no stunboat visits. Shaded ribbons indicate 95% confidence intervals.

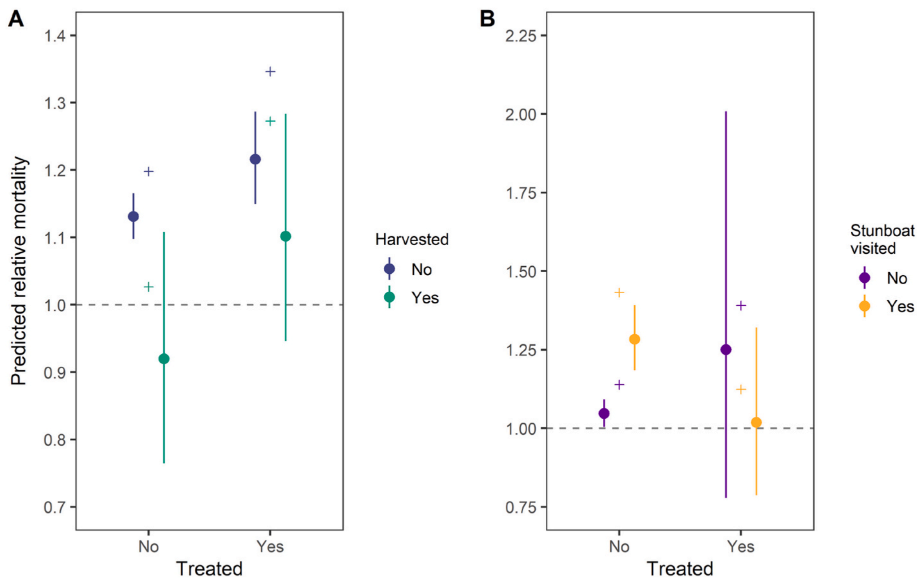

Fig. 7. Adjusted predictions from Model 4A (Panel A) and Model 4B (Panel B) showing the effect of delousing treatments on relative mortality rates in the following month. Crosses indicate the group median value for relative mortality. Panel A shows a significant reduction in relative mortality following months in which some harvest had been conducted, whether or not fish had been treated (production zones 2–13 during 2012–2021: Model 4A). Similarly, Panel B shows that treatment months were followed by elevated relative mortality in production zones 2–7 during 2018–2021 (Model 4B). The effect of stunboats is not significant. Relative mortality is a log rate ratio resulting from actions in month *t*, based on mortality rates in month $t+1$ relative to month $t-1$ (Table 1, Fig. 2). Predicted values in both panels are conditional on no treatment or harvest in months $t-1$ or $t+1$. The predicted values have been back-transformed, and so represent the predicted *n*-fold increase in mortality. Error bars indicate 95% confidence intervals.

of infections and infestations for long enough, and if the health of the cohort is expected to deteriorate or louse levels approach legislated thresholds, farmers may make a decision to treat (if a suitable treatment is available), or else harvest early and forego future growth to avoid risking widespread mortality or regulatory penalties (Pettersen et al., 2015).

Many studies have shown that the fight against salmon lice is driving up the cost of production (Abolofia et al., 2017; Bjørndal and Tusvik, 2020; Iversen et al., 2020; Iversen et al., 2017; Iversen et al., 2015; Kragesteen et al., 2019), and it has been suggested that this fight will drive the industry toward later sea transfers or earlier harvests. (Bjørndal and Tusvik, 2020) modelled scenarios in which steady-state on-growing of 1000 g post-smolts costs 30.8 NOK/kg without delousing and 32.4 NOK/kg with two treatments. After an equivalent production cycle, the scenario with treatments substantially reduces profits via direct costs of treating, higher rates of mortality and downgrading among treated fish, and slower growth due to feeding interruptions (untreated: 2.875 million fish harvested annually at 5.50 kg; treated: 2.847 million at 5.32 kg). However, the optimal strategy depends on the regulatory environment and on-growing costs. If treating is necessary to continue the production cycle, then doing so is likely to be a worthwhile investment, even though the eventual benefit to the farmer will depend on factors such as feed costs (which have been the greatest driver of rising production costs: (Iversen et al., 2017) and how soon the fish will need to be treated again. In general, the fight against salmon lice dominates decision-making in Norwegian salmon aquaculture. The most-used treatment methods are highly stressful for the fish and only effective at removing the mobile louse stages, meaning that louse infestations can return to pre-treatment levels within a few weeks. The never-ending cycle of treatments leads to fatigue among farm personnel (Medaas et al., 2021; Stien et al., 2020), and risks not providing affected fish with sufficient time to recover between treatments, leading to more severe declines in growth and welfare (Moltumyr et al., 2022). This process also occurs amid pressure from authorities, non-government organisations and the general public to keep louse levels down while maintaining good fish health and welfare. The trend toward earlier harvests may therefore reflect ethical and regulatory requirements (i.e. controlling lice while maintaining fish welfare) that are difficult to achieve using available tools (Medaas et al., 2021). In some cases, early harvest may be the best way to avoid criticism.

Another consideration is whether the perceived or actual risks associated with delousing have increased over time. There are a range of diseases that could make early harvest more attractive than delousing, including PD, cardiomyopathy syndrome, amoebic gill disease, and winter ulcers or other lesions (Bang Jensen and Kristoffersen, 2015; Carvalho et al., 2020; Garseth et al., 2018; Oldham et al., 2016; Pettersen et al., 2015; Sommerset et al., 2021; Sviland Walde et al., 2021). Of these, PD has had the greatest increase in reported prevalence, with 100–176 newly positive farms each year from 2013 to 2020 (Sommerset et al., 2021), although a recent requirement for routine testing may account for some of that increase (Ministry of Trade and Industry, 2017b). PD, which is also the only disease reported to the Norwegian Food Authority's database, was associated with a lower probability of treating and a higher probability of harvesting small fish during 2018–2021 in the present analysis. This is suggestive of some risk-aversion when it comes to treating weakened fish. To explore this further, we fitted a supplementary model (Table S14) testing whether farmers are more likely to use freshwater bathing—one of the least effective but gentlest treatments—when the most virulent strain of PD, SAV3, is present at the site. The dataset spanned 2012–2021, but was limited to production zones where SAV3 is tolerated by authorities (zones 2–5) and site-months where some treatment was reported. The model estimated that SAV3 increases the probability of freshwater bathing being the preferred treatment in all 4 zones, from a 5–10% probability in the absence of SAV3 to a 13–23% probability in the presence of SAV3 (Fig. S1).

4.2. *The role of stunboats*

While the rationale for stunboats has been clearly articulated from an industry perspective (Midling et al., 2011; Oaland, 2019; Ringvall, 2020; Sommerset et al., 2021), there is value in characterising their role(s) using industry data on the production parameters and activities that coincide with stunboat visits. Farm-reported data matched to visits by 14 stunboats in 2018–2021 suggests that stunboats were preferred over live fish carriers for small harvest volumes and were sometimes used in stand-by roles during delousing operations, as outlined by recent discussions in the literature (Ringvall, 2020; Sommerset et al., 2021). However, many farming companies prefer to use stunboats for all harvests, even without known complications. There are several possible reasons for this, but foremost are concerns around biosecurity regulations and mortality during crowding, loading and transport. Pancreas disease and cardiomyopathy syndrome are perhaps the most likely to cause mortality at the end of a production cycle, when resulting financial losses are greatest. This is a strong motivator to handle harvest-size fish with extra care. The high prevalence of PD (and we assume also cardiomyopathy syndrome) among harvest-sized fish in southern and western Norway was reportedly a key driver of MOWI's transition to stunboats (Oaland, 2019). Holding pens at slaughterhouses allow some flexibility in the timing of harvesting and transporting, as fish can be delivered by live fish carriers ahead of time and be processed when the slaughterhouse has capacity. However, it is usually illegal to place fish with PD into open holding pens (Ministry of Trade and Industry, 2017b), and while some live fish carriers can transfer fish directly, this is time-consuming. Given the vulnerability of diseased fish to additional stressors, this is likely to result in substantial mortality during transport and transfer. By 2014, MOWI had discontinued use of holding pens, and in 2018, the most southerly of its 4 processing facilities was rebuilt to exclusively receive chilled fish from stunboats (Oaland, 2019). The distribution of stunboats in Norway in late 2020 (all in production zones 1–9: Fig. 5) is consistent with the adoption of stunboats being motivated by the various risk factors that affect harvest-size fish most severely in the southern half of Norway.

It clearly makes sense to slaughter badly injured fish, whether to shorten their suffering or to allow them to be utilised as food. However, stunboats can also be viewed as a 'band-aid' solution to a larger problem: that the predominant delousing methods in use today risk the welfare of farmed salmon. It has been suggested that emergency harvests by stunboats could lead to an underestimation of the welfare impacts of delousing treatments, as injured or moribund fish that are slaughtered before dying are reported to authorities as harvest, not mortality (Sommerset et al., 2021). The present study provides support for that concern, with evidence that: (1) stunboats sometimes visit without any harvest being reported, which may be indicative of a standby role (Fig. 4); (2) stunboat visits predict harvests of small fish, as may occur following a risky delousing treatment (Model 3B, Fig. 6B); and (3) harvests during treatment months lead to a smaller increase in mortality than would otherwise be expected (Fig. 7A). Moreover, while Model 4B (Fig. 7B) did not find stunboat visits to be a significant predictor of relative mortality, we suspect that a larger sample size would have revealed a stunboat effect that interacts with treatment status. For farms with fish well below harvest size, visits by stunboats during non-treatment months are probably a response to disease outbreaks or other health problems. In such cases, stunboat visits would correlate with higher relative mortality if not all affected fish are harvested or poor environmental conditions persist. By contrast, stunboat visits during treatment months may result in relatively low mortality rates if the stunboat arrives before treatment begins and is able to selectively harvest any fish not to be treated and/or salvage fish that were injured during treatment. However, we note that among site-months in 2018–2021 where the fish were between 0.25 and 3.5 kg and some treatment was reported, relatively few coincided with stunboat visits (182 out of 2030 treatment months). Most stunboat visits were to sites with cohorts that were closer to an ideal harvest size (median 3.9 kg across 774 site-months in 2018–2021). Those visits likely reflect a range of motivations that are not easily distinguished based on the available data, including standard harvests, standby roles during delousing, harvesting of sick or vulnerable fish (unrelated to delousing), and for overstocked sites, spot harvesting to remain within biomass or density caps.

Drivers of early harvest, as well as the possible influence of stunboats on treatment decisions, warrant further attention in the future as more stunboats are commissioned. Future studies would benefit from access to cage-specific harvests and mortalities, as well as comprehensive veterinary data on disease status and other mortality risk factors (Persson et al., 2021; Sviland Walde et al., 2021). Early harvest is a valid welfare mitigation strategy that has benefitted from the availability of stunboats. However, in an ideal world, stunboats would be reserved as welfare-friendly alternatives to live fish carriers. Their current role underlines the importance of developing cost-effective strategies to prevent infestations and more welfare-friendly delousing methods.

CRediT authorship contribution statement

LukeT. Barrett: Conceptualization, Methodology, Formal analysis, Writing – original draft. **Tina Oldham:** Writing – review & editing. **Tore S. Kristiansen:** Writing – review & editing, Project administration. **Frode Oppedal:** Writing – review & editing. **Lars H. Stien:** Conceptualization, Methodology, Data curation, Writing – review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2022.738440.

References

Aaen, S.M., Helgesen, K.O., Bakke, M.J., Kaur, K., Horsberg, T.E., 2015. Drug resistance in sea lice: a threat to salmonid aquaculture. Trends Parasitol. 31, 72–81.

Abolofia, J., Asche, F., Wilen, J.E., 2017. The cost of lice: quantifying the impacts of parasitic sea lice on farmed salmon. Mar. Resour. Econ. 32, 329–349.

Asche, F., Sikveland, M., Zhang, D., 2018. Profitability in Norwegian salmon farming: the impact of firm size and price variability. Aquac. Econ. Manag. 22, 306–317.

Bang Jensen, B., Kristoffersen, A.B., 2015. Risk factors for outbreaks of infectious pancreatic necrosis (IPN) and associated mortality in Norwegian salmonid farming. Dis. Aquat. Org. 114, 177–187.

Barrett, L.T., Oppedal, F., Robinson, N., Dempster, T., 2020. Prevention not cure: a review of methods to avoid sea lice infestations in salmon aquaculture. Rev. Aquac. 12, 2527–2543.

Berge, A., 2021. Manko på Storlaks Drar Med Seg Prisene Oppover. iLaks.no. https://ilaks.no/manko-pa-storlaks-drar-med-seg-prisene-oppover (Last accessed: 11 Mar 2022).

Bjørndal, T., Tusvik, A., 2020. Economic analysis of on-growing of salmon post-smolts. Aquac. Econ. Manag. 0, 1–32.

Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A., Bolker, B., 2017. GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400.

Cantrell, D., Filgueira, R., Revie, C.W., Rees, E.E., Vanderstichel, R., Guo, M., Grant, J., 2020. The relevance of larval biology on spatiotemporal patterns of pathogen connectivity among open-marine salmon farms. Can. J. Fish. Aquat. Sci. 77, 505–519.

Carvalho, L.A., Whyte, S.K., Braden, L.M., Purcell, S.L., Manning, A.J., Muckle, A., Fast, M.D., 2020. Impact of co-infection with *Lepeophtheirus salmonis* and *Moritella viscosa* on inflammatory and immune responses of Atlantic salmon (*Salmo salar*). J. Fish Dis. 43, 459–473.

Coates, A., Phillips, B.L., Bui, S., Oppedal, F., Robinson, N.A., Dempster, T., 2021. Evolution of salmon lice in response to management strategies: a review. Rev. Aquac. 13, 1397–1422.

Coretta, S., 2021. tidymv: Tidy Model Visualisation for Generalised Additive Models. R Package Version 3.3.0.

Dempster, T., Overton, K., Bui, S., Stien, L.H., Oppedal, F., Karlsen, Ø., Barrett, L.T., 2021. Farmed salmonids drive the abundance, ecology and evolution of parasitic salmon lice in Norway. Aquac. Environ. Interact. 13, 237–248.

Forsberg, O.I., Guttormsen, A.G., 2006. The value of information in salmon farming. Harvesting the right fish at the right time. Aquac. Econ. Manag. 10, 183–200.

Fox, J., Weisberg, S., 2019. An {R} Companion to Applied Regression, 3rd ed. Sage, Thousand Oaks, California.

Garseth, Å.H., Fritsvold, C., Svendsen, J.C., Bang Jensen, B., Mikalsen, A.B., 2018. Cardiomyopathy syndrome in Atlantic salmon *Salmo salar* L.: a review of the current state of knowledge. J. Fish Dis. 41, 11–26.

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

Grøntvedt, R.N., Nerbøvik, I.-K.G., Viljugrein, H., Lillehaug, A., Nilsen, H., Gjevre, A.-G., 2015. Thermal de-Licing of Salmonid Fish - Documentation of Fish Welfare and Effect, vol. No. 13. Norwegian Veterinary Institute.

Hartig, F., 2019. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R Package Version 0.2.2.

Iversen, A., Hermansen, Ø., Andreassen, O., Brandvik, R.K., Marthinussen, A., Nystøyl, R., 2015. Kostnadsdrivere i Lakseoppdrett. Nofima Report 41/2015. https://nofima.no/publikasjon/1281065/.
Iversen, A., Hermansen, Ø., Nystøyl, R., Hess, E.J., 2017. Kostnadsutvikling i Lakseoppdrett – med Fokus på fôr- og Lusekostnader. Nofima Report 24/2017. https://nofima.no/publikasjon/1523319/.
Iversen, A., Asche, F., Hermansen, Ø., Nystøyl, R., 2020. Production cost and competitiveness in major salmon farming countries 2003–2018. Aquaculture 522, 735089.
Johansen, L.-H., Jensen, I., Mikkelsen, H., Bjørn, P.-A., Jansen, P.A., Bergh, Ø., 2011. Disease interaction and pathogens exchange between wild and farmed fish populations with special reference to Norway. Aquaculture 315, 167–186.
Kragesteen, T.J., Simonsen, K., Visser, A.W., Andersen, K.H., 2019. Optimal salmon lice treatment threshold and tragedy of the commons in salmon farm networks. Aquaculture 512, 734329.
Kristoffersen, A.B., Qviller, L., Helgesen, K.O., Vollset, K.W., Viljugrein, H., Jansen, P.A., 2018. Quantitative risk assessment of salmon louse-induced mortality of seaward-migrating post-smolt Atlantic salmon. Epidemics 23, 19–33.
Lüdecke, D., 2018. Ggeffects: tidy data frames of marginal effects from regression models. J. Open Source Softw. 3, 772.
Medaas, C., Lien, M.E., Gismervik, K., Kristiansen, T.S., Osmundsen, T., Størkersen, K.V., Stien, L.H., 2021. Minding the gaps in fish welfare: the untapped potential of fish farm workers. J. Agric. Environ. Ethics 34, 29.
Midling, K.Ø., Harris, S., Humborstad, O.B., Akse, L., Noble, C., Evensen, T.H., Tobiassen, T., 2011. Slakting Direkte fra Oppdrettsmerd.Tauranga – fase 3. Nofima Report 44/2011. https://nofima.no/publikasjon/1161215/.
Ministry of Trade and Industry, 2008. Forskrift om Drift av Akvakulturanlegg (Akvakulturdriftsforskriften) (No. FOR-2008-06-17–822).
Ministry of Trade and Industry, 2012. Forskrift om Bekjempelse av Lakselus i Akvakulturanlegg (No. FOR-2012-12-05-1140).
Ministry of Trade and Industry, 2017a. Forskrift om Produksjonsområder for Akvakultur av Matfisk i sjø av Laks, Ørret og Regnbueørret (Produksjonsområdeforskriften) (No. FOR-2017-01-16-61).
Ministry of Trade and Industry, 2017b. Forskrift om Tiltak for å Forebygge, Begrense og Bekjempe Pankreassykdom (PD) hos Akvakulturdyr (No. FOR-2017-08-29-1318).
Moltumyr, L., Nilsson, J., Madaro, A., Seternes, T., Winger, F.A., Rønnestad, I., Stien, L.H., 2022. Long-term welfare effects of repeated warm water treatments on Atlantic salmon (Salmo salar). Aquaculture 548, 737670.
Noble, C., Gismervik, K., Iversen, M.H., Kolarevic, J., Nilsson, J., Stien, L.H., Turnbull, J.F., 2018. Welfare Indicators for Farmed Atlantic Salmon: Tools for Assessing Fish Welfare, 351 pp. https://nofima.no/publikasjon/1636395/.
Oaland, Ø., 2019. Processing boats - an improvement for fish health and fish welfare. In: Seminar on Biosecurity and Transportation of Fish, 19 Aug 2019, Trondheim. https://www.vetinst.no/arrangementer/biosecurity-and-transportation-of-fish.
Oldham, T., Rodger, H., Nowak, B.F., 2016. Incidence and distribution of amoebic gill disease (AGD) — an epidemiological review. Aquaculture 457, 35–42.
Oliveira, V.H.S., Dean, K.R., Qviller, L., Kirkeby, C., Bang Jensen, B., 2021. Factors associated with baseline mortality in Norwegian Atlantic salmon farming. Sci. Rep. 11, 14702.
Overton, K., Dempster, T., Oppedal, F., Kristiansen, T.S., Gismervik, K., Stien, L.H., 2019. Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. Rev. Aquac. 11, 1398–1417.
Pedersen, E.J., Miller, D.L., Simpson, G.L., Ross, N., 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. PeerJ 7, e6876.
Persson, D., Nødtvedt, A., Aunsmo, A., Stormoen, M., 2021. Analysing mortality patterns in salmon farming using daily cage registrations. J. Fish Dis. 45, 335–347.
Pettersen, J.M., Rich, K.M., Jensen, B.B., Aunsmo, A., 2015. The economic benefits of disease triggered early harvest: a case study of pancreas disease in farmed Atlantic salmon from Norway. Prev. Vet. Med. 121, 314–324.
R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Ringvall, J.L., 2020. Mobile Slaughterhouses at Sea - Do Stun-and-Bleed Vessels Meet Norwegian Salmon Farming Requirements? Master Thesis. NTNU. https://ntnuopen.ntnu.no/ntnu-xmlui/handle/11250/2780078.
Roth, B., 2016. Avlusing av Laksefisk Med Optilice: Effekt på avlusing og fiskevelferd. Nofima Report 59/2016. https://nofima.no/publikasjon/1408716/.
Samsing, F., Johnsen, I., Dempster, T., Oppedal, F., Treml, E.A., 2017. Network analysis reveals strong seasonality in the dispersal of a marine parasite and identifies areas for coordinated management. Landsc. Ecol. 32, 1953–1967.
SjømatNorge, 2020. Akvafakta Måned - Desember 2020. https://akvafakta.no/wp-content/uploads/Maned/2020/2012_Akvafakta.pdf.
Sommerset, I., Bang Jensen, B., Bornø, G., Haukaas, A., Brun, E., 2021. Fiskehelserapporten 2020. Norwegian Veterinary Institute. https://www.vetinst.no/rapporter-og-publikasjoner/rapporter/2021/fiskehelserapporten-2020.
Stien, L.H., Bracke, M.B.M., Folkedal, O., Nilsson, J., Oppedal, F., Torgersen, T., Kristiansen, T.S., 2013. Salmon welfare index model (SWIM 1.0): a semantic model for overall welfare assessment of caged Atlantic salmon: review of the selected welfare indicators and model presentation. Rev. Aquac. 5, 33–57.
Stien, L.H., Lind, M.B., Oppedal, F., Wright, D.W., Seternes, T., 2018. Skirts on salmon production cages reduced salmon lice infestations without affecting fish welfare. Aquaculture 490, 281–287.
Stien, L.H., Tørud, B., Gismervik, K., Lien, M.E., Medaas, C., Osmundsen, T., Størkersen, K.V., 2020. Governing the welfare of Norwegian farmed salmon: three conflict cases. Mar. Policy 117, 103969.
Størkersen, K.V., Osmundsen, T.C., Stien, L.H., Medaas, C., Lien, M.E., Tørud, B., Gismervik, K., 2021. Fish protection during fish production. Organizational conditions for fish welfare. Mar. Policy 129, 104530.
Sviland Walde, C., Bang Jensen, B., Pettersen, J.M., Stormoen, M., 2021. Estimating cage-level mortality distributions following different delousing treatments of Atlantic salmon (salmo Salar) in Norway. J. Fish Dis. 44, 899–912.
Taranger, G.L., Karlsen, Ø., Bannister, R.J., Glover, K.A., Husa, V., Bjørn, A., Sva, T., 2015. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. J. Mar. Sci. 72, 997–1021.
Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O.T., Nilsen, F., Jackson, D., 2013. Salmon lice - impact on wild salmonids and salmon aquaculture. J. Fish Dis. 36, 171–194.
Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.
Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B Stat Methodol. 73, 3–36.