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Salmon lice (*Lepeophtheirus salmonis*) in the stomach contents of lumpfish (*Cyclopterus lumpus*) sampled from Norwegian fish farms: Relationship between lice grazing and operational conditions

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ABSTRACT

Cleaner fish are commonly used as a control measure against salmon lice infestations in salmonid farms. Lumpfish (*Cyclopterus lumpus*) is the most common cleaner fish species used in Norwegian farms. However, little is known about how different operational, including environmental, conditions affect the salmon lice grazing efficacy by lumpfish. In this paper, we analyse salmon lice (*Lepeophtheirus salmonis*) in the stomach contents of a large sample of more than 20,000 lumpfish from 80 different Norwegian farms. We investigate the proportion of lumpfish with salmon lice and the mean number of salmon lice in the stomach contents of the lumpfish. We further explore how the salmon lice contents vary with different factors like lumpfish weight, weight of salmonids, salmon lice abundance in the cage, cloud cover, and sea temperature. We find that 3.1% of the 24,693 lumpfish contained salmon lice. Most of the lumpfish with salmon lice in their stomach contents contained few (one or two) lice, while there were a few lumpfish which contained many salmon lice. We find more salmon lice in the stomach contents with increasing abundance of salmon lice in the sea cage, lower weight of the salmonids, and in clear weather. Interestingly, for the relationship between lumpfish weight and salmon lice in the stomach contents, we find increased salmon lice grazing from ca. 5 g up to an optimal weight of ca. 40 g, and then a decrease from 40 g. Surprisingly, we find no relationship between sea temperature and salmon lice per lumpfish. We find more salmon lice in the stomach contents of the lumpfish with comparatively high condition. By studying the factors associated with most efficient salmon lice grazing, our paper contributes to understanding how different operational factors affect salmon lice grazing by lumpfish. For controllable factors, the results thus contribute to guiding the best practice for use of lumpfish as a salmon lice control measure.

1. Introduction

Salmon lice infestation is a problem for the fish farming industry in terms of great economic costs, fish health burden both on farmed and wild fish, and is damaging for the public perception of farmed fish (Costello, 2009; Brooker et al., 2018a, 2018b; Torrissen et al., 2013).

The use of cleaner fish is a popular control measure against salmon lice (Powell et al., 2018; Brooker et al., 2018b), and considered an attractive alternative to for example medical treatments, with lower costs, and likely less stress induced on the farmed salmonids (Treasurer, 2002). Moreover, cleaner fish are also used to reduce the use of other treatments, and could delay or even prevent the development of resistance to for example new medical treatments. For low temperatures, lumpfish (*Cyclopterus lumpus*) is the most popular cleaner fish species, as wrasse tend to become inactive (Powell et al., 2018; Imsland et al., 2016a; Brooker et al., 2018b). Lumpfish are thus the most common cleaner fish species in Norwegian farms (Barrett et al., 2020; Fiskeridirektoratet, 2021).

A typical Norwegian salmonid farm consists of approximately eight floating net pen cages (Aldrin et al., 2017), open to salmon lice

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transmission. In Norway, all farms are required by law to perform weekly lice counts in all cages (Norwegian Ministry of Trade, Industry and Fisheries, 2012). The lice abundance averaged over all cages are reported to the Norwegian Food Safety Authority and are openly available through the website BarentsWatch (BarentsWatch, 2022). Lumpfish used as cleaner fish in salmon farms are of farm origin. They are typically grown to sizes of 20–50 g in tanks on land, and then released into the net pen cages along with farmed salmonids at stocking densities of roughly 3–10% of the numbers of farmed salmonids in the cages (Imsland et al., 2018; Skiftesvik et al., 2021). They are also normally provided with shelter in the form of plastic imitations of seaweed in the cages and fed artificial fish feed. However, many knowledge gaps remain with respect to good practice husbandry of lumpfish in large scale salmonid cages (Skiftesvik et al., 2021).

Many experimental studies report that lumpfish efficiently control salmon lice infestation levels on farmed salmonids (Imsland et al., 2014a, 2014b, 2014c, 2016b, 2018; Imsland and Reynolds, 2022). A recent review of the evidence-base for sea lice removal by cleaner fish in salmon aquaculture, however, found a restricted number of studies comparing lice removal in cages with and without cleaner fish in a replicated experimental design. Most studies were conducted with insufficient replication and in small scale cages compared to commercial scale cages (Overton et al., 2020). Moreover, a recent study using the national scale BarentsWatch database of louse counts, delousing treatments, and cleaner fish stocking events on Norwegian salmon farms, only found small and highly variable effects of cleaner fish on (i) the timing of the first delousing event and (ii) louse population growth rates (Barrett et al., 2020). Both latter studies point to the need for a better understanding of factors affecting delousing efficacy in commercial sea cages to adopt more targeted, evidence-based use of cleaner fish in salmon aquaculture (Overton et al., 2020; Barrett et al., 2020).

A different approach to studying lumpfish cleaning is to consider the stomach contents of the lumpfish during production. Imsland et al. (2014a, 2015) found that 10–38% of the sampled lumpfish contained sea lice. Imsland et al. (2016b) generally found a lower percentage of lumpfish stomachs containing sea lice (0–25%), but significantly higher percentages in the smallest of three size groups of lumpfish (initial mean ca. 23 g). All these studies were, however, conducted in small scale net pens (5 × 5 × 5 m). Eliasen et al. (2018) analysed the stomach contents of 5511 lumpfish over a period of approximately two years from commercial Faroese salmon farms. Altogether, 13.5% of these fish contained sea lice. The prevalence of sea lice in the stomach contents decreased in the summer months, corresponding with an increase in the abundance of zooplankton. Also, the mean weight of lumpfish containing sea lice was smaller than those not containing sea lice, indicating that smaller lumpfish are more efficient sea lice grazers than larger lumpfish (Eliasen et al., 2018).

In this study, we analyse a database of stomach contents in more than 20,000 lumpfish from 80 different Norwegian farms. The farmed fish are salmonids, i.e. either Atlantic salmon (*Salmo salar*) or rainbow trout (*Oncorhynchus mykiss*). We analyse how different factors relate to the number of salmon lice in the stomach contents. We perform a multiple nonlinear statistical regression analysis, analysing effects of salmon lice abundance in the sea cages, cloud cover, salmonid weight, sea temperature, and lumpfish weight. We also analyse the effect of lumpfish density and lumpfish condition factor.

To our knowledge, the present data represent the largest sample of lumpfish stomach contents that has been analysed. Through this analysis, we provide evidence of which operational conditions are most beneficial for salmon lice grazing by lumpfish, for the factors analysed in this study. Hence, for the controllable factors, the results can be used to guide fish farmers on appropriate use of lumpfish as a control measure for salmon lice.

2. Data

The data consist of 26,850 unique observations of lumpfish with information on lumpfish length, lumpfish weight, stomach contents, locality, sampling date, cloud cover (clear weather, partly clouded, clouded), sea temperature at 5 m depth, average weight of salmonids, lumpfish density (ratio between the number of lumpfish and the number of salmonids), salmon lice per salmonid in the cage (salmon lice abundance, all stages except chalimus), and lumpfish capture method (trap or dip net). The observations are from multiple sea cages from each locality (average per visit 1.7, standard deviation 1.7, range 1 to 13). The abundance of salmon lice per salmonid in the sea cage is reported in the data as an average over a sample of salmonids, where the numbers of pre-adult and adult salmon lice are counted. We will only consider the total number of pre-adult and adult lice on the salmonids, hereafter denoted as salmon lice abundance.

In the stomach contents, we will consider the numbers of salmon lice of all stages (*Lepeophtheirus salmonis*). As other examples of stomach content, the lumpfish contained mainly lumpfish feed, fouling, jellyfish, *Calanus*, other copepods, and salmon feed. The data also contain counts of sea lice of the species *Caligus elongatus*, which we do not focus on in the present study. A brief overview of the *Caligus elongatus* counts is provided in the supplementary material section S4.1.

Some observations are filtered out, due to biologically extreme, impossible, or unlikely values. Moreover, the analyses require complete observations, i.e. no missing values of the variables considered. Hence, for the different analyses, we also filter out observations with missing values on one or more of the variables considered. We also filter out the lumpfish that were registered as dead upon sampling (830 lumpfish).

The details on how we chose to filter the data are provided in the supplementary material. The data set which is used for analysing the overall amount of salmon lice in the stomach contents of the lumpfish consists of 24,693 observations after filtering. In total, we have data from 80 fish farms in Norway between 2016-08-11 and 2022-01-17. The observations are distributed over 1041 visits, with an average of 13 visits for each location (standard deviation 11.4, range 1 to 43). There are on average 23.7 lumpfish sampled in each visit (standard deviation 19.3, range 1 to 299).

In Norway, the salmonid farms are divided into 13 different production areas, and a map of production areas can be found in the supplementary material. The distribution of observations across calendar months and production areas is provided in Table 1. We note that we only have observations from seven of the 13 production areas, and that most observations are from production area 3 (Western Norway) and 11 (Northern Norway). All calendar months are represented, though there are fewest observations during the winter months.

In the main regression analysis, including the explanatory variables lumpfish weight, cloud cover, sea temperature, salmonid weight, and salmon lice abundance, we end up with 20,048 complete observations.

Table 1
Number of observations per production area, calendar month, and year. For the missing production areas, there were no observations.

Observations per production area (PA) over 2016–2022							
PA	1	3	4	6	7	11	13
Observations	822	11,433	1650	783	20	9112	873
Observations per calendar month over 2016–2022, all PA combined							
Month	1	2	3	4	5	6	7
Observations	1456	1174	1067	1988	2753	3254	3279
Month	8	9	10	11	12		
Observations	2428	2148	2208	1611	1327		
Observations per year, all PA combined							
Year	2016	2017	2018	2019	2020	2021	2022
Observations	188	129	812	1732	7830	13,395	607

The data set used to analyse lumpfish density consists of 18,498 complete observations.

2.1. Condition factor

We also investigate how the number of salmon lice in the stomach contents relates to the condition factor of the lumpfish. A standardised definition for measuring the length of the lumpfish is necessary for this analysis, as we compare lumpfish of different lengths. A standardised procedure was implemented on 2020-04-01, with instructions to measure the length only to the caudal peduncle, not including the caudal fin (i.e. potential erosion). Hence, in this analysis, we only consider lumpfish sampled after 2020-04-01. Five fish farms did not adhere to the new standard, and we thus disregard these farms. We end up with 17,902 observations in this analysis.

The condition factor is calculated as a function of length and weight. We use an expression for the condition factor derived from the analysis in Gutierrez-Rabadan et al. (2021), K_R, given by

$$K_R = W/L^{2.559},$$

where W and L are the weight measured in grams and length of the lumpfish measured in centimetres. Gutierrez-Rabadan et al. (2021) tuned this condition factor to fit the shape of lumpfish post-deployment (Note that Gutierrez-Rabadan et al. (2021) also included a proportionality factor that we have ignored here.)

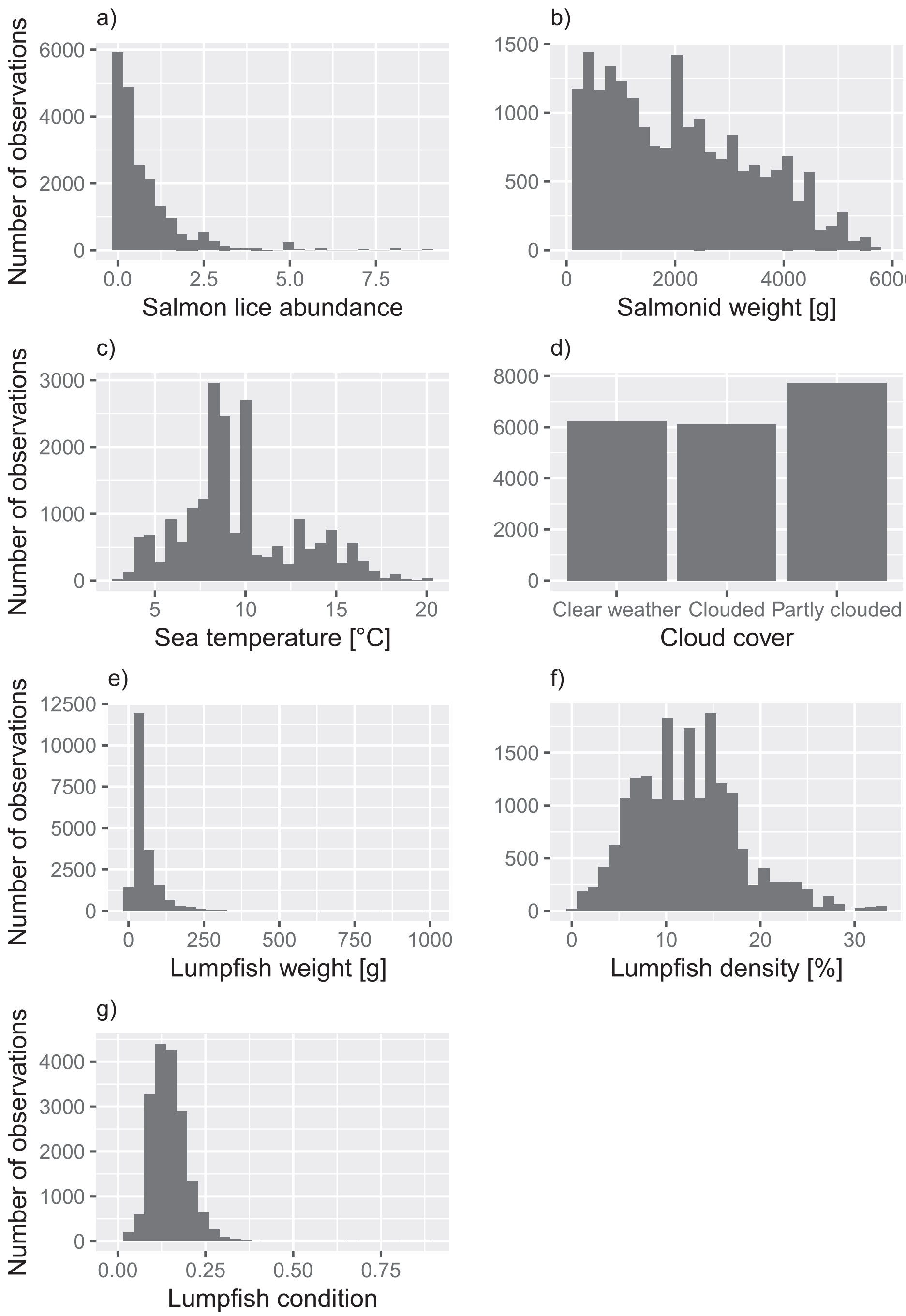

Fig. 1. Data overview. Histogram of the different covariates in the data.

2.2. Overview of observations

An overview of the different variables in the data after filtering is provided in Fig. 1.

2.3. Software design

The data collection system was created as a single-page online digital form in order to minimise the likelihood of data loss. Responsive design was applied in order to fit tablet, personal computer, and mobile phone screens, as well as analogous printout paper form. Further, in order to motivate the field operator, a minimal data analysis response form was developed, displaying in real-time a summary of the newly recorded data presented along with a simple analysis showing how the new records compared with historical data.

2.4. Data recording

The instructions for the different variables in the digital form was:

- Salmon lice per lumpfish at individual level: number of salmon lice of all stages identified in the stomach contents of the lumpfish.
- Lumpfish length measured in centimetres. From 2020-04-01, the instructions were to measure the length only to the caudal peduncle.
- Lumpfish weight measured in grams.
- Sea temperature at locality level measured at 5 m depth on the day of sampling.
- Lumpfish density at cage level: Estimated as the number of deployed lumpfish minus the number of dead lumpfish (registered), divided by the number of salmonids in each cage.
- Cloud cover on the day of sampling at locality level as one out of three categories: clear weather, partly clouded, or clouded.
- Abundance of pre-adult and adult salmon lice per salmonid: mean total number of pre-adult and adult salmon lice per salmonid at cage level.
- Average weight of salmonids at cage level.

3. Regression models

To analyse the relationship between the salmon lice quantity per lumpfish and the various covariates, we fit generalised additive models (Hastie and Tibshirani, 1990) allowing flexible functions for the covariate effects. We chose to use the negative binomial distribution for the response, in accordance with overdispersed count data. We use the implementation in the R-package mgcv (Wood, 2021, version 1.8–38).

We model the logarithm of the expected number of salmon lice per lumpfish, μ, as

$$log\mu = \beta_0 + s(x_1) + \ldots + s(x_p) + \beta_{pc}x_{pc} + \beta_c x_c + \gamma_l,$$

where β_0 is the intercept, $x_1, \ldots, x_p$ are the p continuous covariates, the s's are smooth, continuous functions to be estimated, and γ_l is a random intercept term in locality. We estimate a main model where the continuous covariates are lumpfish weight, sea temperature, salmonid weight, and salmon lice abundance. We also estimate two alternative models: one with lumpfish density, and another with lumpfish condition factor, in addition to the covariates included in the main model. The parameters β_{pc} and β_c are the effects of partly clouded and clouded weather, respectively, relative to clear weather, and x_{pc} and x_c are indicator variables for partly clouded and clouded weather, respectively. The random effect in locality is included to take into account the fact that observations from the same locality may not be reasonable to treat as independent observations, even after adjusting for the various other covariates in the model. As we model the logarithm of the expectation, this means that we have a multiplicative model on the original scale. Additional details on the covariate transformations and smoothing parameter specification of the estimated effects are provided in the supplementary material.

All the plots of the estimated effects from the fitted regression models are produced using the R-package sjPlot (Lüdecke, 2021, version 2.8.10).

4. Results

4.1. Salmon lice contents

Out of the 24,693 lumpfish, only 3.1% contained salmon lice. The average number of salmon lice per lumpfish was 0.19 (standard deviation 2.8, range 0 to 148). Out of those that contained salmon lice, the average number of salmon lice was 6.1 (standard deviation 15). A histogram of the number of salmon lice in the stomach contents is provided in Fig. 2, only including the lumpfish which contained at least one salmon louse. We note that out of the lumpfish that contained salmon lice, most contained one louse, while there were a few lumpfish with many salmon lice in the stomach contents.

4.2. Results from regression models

4.2.1. Main model

We fitted the regression model to the 20,048 lumpfish observations. The resulting covariate effects are provided in Fig. 3. The figure shows the expected number of salmon lice in the stomach contents per lumpfish, along with 95% confidence bands, as a function of each continuous covariate when all the other continuous covariates are fixed at their average value in the data, and with cloud cover set to clear weather, for an average locality (i.e. the locality with estimated intercept closest to zero). We found that the number of salmon lice in the stomach contents increased from ca. 0.15 to 0.4 with increasing abundance of salmon lice, until around a salmon lice abundance of two pre-adult and adult salmon lice per salmonid (Fig. 3a). For larger values of salmon lice abundance, the estimated function was rather constant, but note that the uncertainty increased. This was because almost all observations of salmon lice abundance were below 2.5 (cf. Fig. 1a). The number of salmon lice per lumpfish sample increased with salmonid weight (Fig. 3b). We did not find an effect of sea temperature on the amount of salmon lice in the stomach contents (Fig. 3c). The estimated effect had a large uncertainty and was far from statistically significant. The amount of salmon lice per lumpfish was larger for clear weather than clouded weather, with an estimated difference of ca. 0.1 (Fig. 3d). For lumpfish weight, we found an optimal weight of 41 g (Fig. 3e). Hence for lumpfish weights up to 41 g, we found an increase in the number of salmon lice per lumpfish from approximately 0.05 to 0.3. For weights larger than 41 g, the number of salmon lice per lumpfish decreased quickly. For weights above 250 g, the uncertainty was large, as there were few observations above this level.

Predictions from model. We used the fitted model to predict the number of salmon lice per lumpfish for a selection of values of the different covariates. Specifically, we computed the expected number of salmon lice per lumpfish for lumpfish weights of 40 g and 100 g, salmon lice abundance of 0.1 and 1.0, sea temperature of 10 °C, salmonid weight of 1000 g, an average locality, and a weighted average of cloud cover according to the frequency in the observed data.

For an abundance of 0.1 salmon lice per salmonid, the expected number of salmon lice per lumpfish was found to be 0.095 and 0.051, for lumpfish weight 40 g and 100 g, respectively. For an abundance of 1.0 salmon lice per salmonid, the expected number of salmon lice per lumpfish was found to be 0.19 and 0.10 for lumpfish weight 40 g and 100 g, respectively.

4.2.2. Model including lumpfish density

We fitted the regression model with the same covariates, but in addition including the lumpfish density. The resulting continuous effect

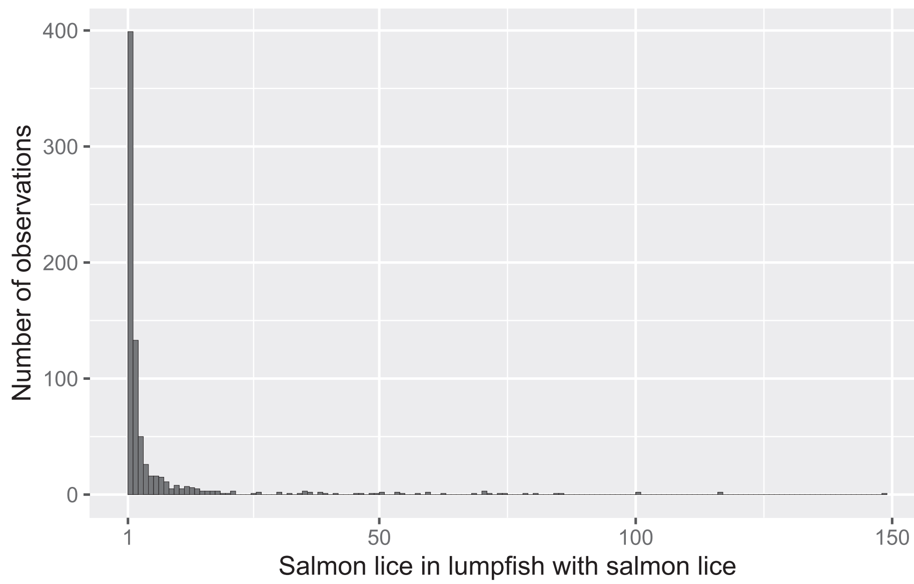

Fig. 2. Salmon lice counts. Histogram of salmon lice quantity in the lumpfish stomachs, for those that contained at least one louse.

of lumpfish density is provided in Fig. 4a. The other estimated effects did not change qualitatively when also adjusting for the density of lumpfish (see the supplementary material). There was no clear evidence of an effect of lumpfish density on salmon lice in the lumpfish stomach contents, even though the estimated effect was slightly increasing with lumpfish density, but note the large uncertainty.

4.2.3. Model including lumpfish condition factor

We also fitted the regression model including lumpfish condition as an additional covariate. The resulting effect of lumpfish condition is provided in Fig. 4b. We found an increasing effect of the condition, with comparably more salmon lice in the stomach contents in lumpfish with high condition factors. When the condition factor increased from 0.1 to 0.3, the expected number of salmon lice per lumpfish increased from approximately 0.2 to 0.5. The average lumpfish condition factor in the data was 0.15 (standard deviation 0.053, range 0.012 to 0.9). The other effects can be found in the supplementary material, and in general they did not change qualitatively compared to the main model when also controlling for lumpfish condition.

5. Discussion

By analysing a large database containing samples of stomach contents from lumpfish used as cleaner fish in Norwegian salmon farms, we have identified relationships between different operational factors and salmon lice grazing efficacy. This contributes to understanding the effect of different operational conditions, which can guide optimal operational conditions for the factors that the fish farmers can control. It also contributes to explaining some of the observed heterogeneities in sea lice grazing by individual lumpfish.

5.1. Estimated covariate effects

5.1.1. Salmon lice abundance

We found more salmon lice in the stomach contents of lumpfish with increasing abundance of salmon lice, up to a threshold of about two pre adult and adult salmon lice per salmonid. Beyond that, we found no increasing effect of salmon lice abundance in the sea cages, matching a Holling's type II functional response (Holling, 1959). One potential explanation is that interestingly, even at salmon lice abundance above two pre-adult and adult salmon lice per salmonid, only around 3% of the lumpfish contained salmon lice. This may suggest that most lumpfish never develop the ability to graze salmon lice of salmonid hosts in full scale commercial cages, irrespective of the availability of lice. Moreover, it is known that the increase in the number of prey consumed by a predator as a function of prey density will ultimately level off (Holling, 1959), and the results may indicate that the lumpfish that do graze on salmon lice are satiated at relatively low prey densities. Another contributing factor could be potential behavioural changes in salmon with high lice abundance, which can affect the interaction between the lumpfish and the salmonids. For example, salmon have been found to swim comparably deeper during nighttime with higher lice prevalence (Bui et al., 2016), which may make lice grazing more difficult for the lumpfish (Geitung et al., 2020; Leclercq et al., 2018). Regardless of the causal mechanisms, the results imply that the proportion of the lice being eaten by lumpfish is lowest at high lice abundance. Hence, the potential for controlling lice numbers by lumpfish decreases with increasing abundance of lice on the salmonid hosts.

5.1.2. Salmonid weight

We found more salmon lice in the lumpfish stomachs for higher salmonid weight. This could be because larger pellets are used to feed the salmon as they become larger, so that the pellet size is too large for the lumpfish. Salmon pellets have previously been found to be one of the main items in lumpfish diets (Imsland et al., 2015). Note that there might also be confounding between salmonid weight and salmon lice abundance, through time since deployment, as salmon lice abundance correlates positively with salmon weight (Jansen et al., 2012; Aldrin et al., 2019). The effect of salmonid weight could also be confounded with time since deployment due to habituation effects. As there is considerable uncertainty associated with the lice counts (e.g. Aldrin et al., 2017), salmonid weight may capture variation in lice abundance not captured by the counts. Another potential explanation is possible changes in behavioural interactions between lumpfish and small and large salmonids.

5.1.3. Sea temperature

Surprisingly, we found no association between sea temperature and the number of salmon lice in the lumpfish stomach contents. Hence, we are unable to confirm the experience from the industry that lumpfish prefer low temperatures (Brooker et al., 2018b). However, to our knowledge, there are no studies comparing salmon lice grazing by lumpfish at different temperatures. There are, however, studies which show that lumpfish mortality increases when the temperatures become

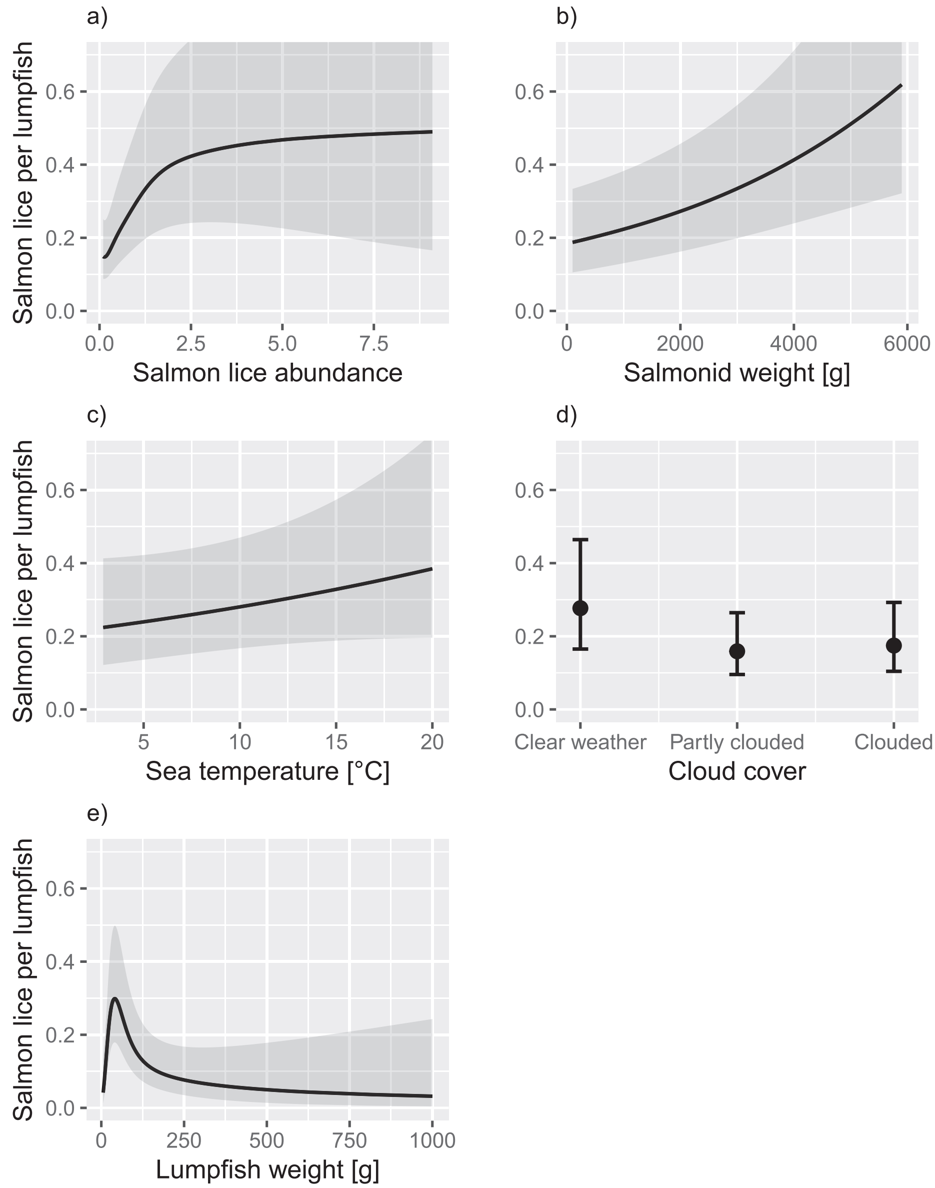

Fig. 3. Estimated covariate effects and 95% confidence bands. The covariates are salmon lice abundance (a), salmonid weight (b), sea temperature (c), cloud cover (d), and lumpfish weight (e).

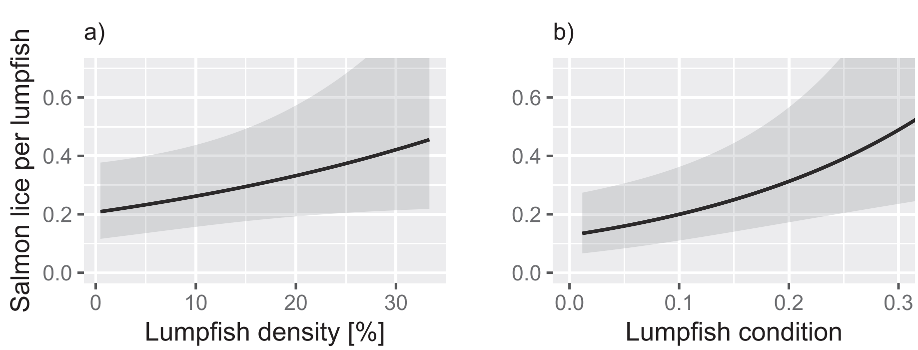

Fig. 4. Estimated covariate effects and 95% confidence bands of lumpfish density and condition. The panels show the effects of lumpfish density (a) and lumpfish condition (b) in the fitted generalised additive models. Note that for condition factor, we only show the figure for values up to 0.3, as the uncertainty becomes very large for the few observations above 0.3.

too low (Imsland et al., 2018, below 4 °C) or too high (Nytrø et al., 2014; Hvas et al., 2018, 13–16 °C). Moreover, Hvas et al. (2018) found that while lumpfish were still observed feeding at temperatures above 18 °C, their behaviour was found to be erratic and cataract formation in their eyes was observed, which could affect their salmon lice grazing efficacy. Sea temperature could also affect the interaction between the lumpfish and salmonids through affecting their species-specific preferred swimming depths (Oppedal et al., 2011; Geitung et al., 2020). Note also that the intuition and perceived effects are cluttered by the fact that sea temperature is confounded with salmon lice abundance in the cages. Hence, it is hard to tease out the effect of sea temperature without conducting analyses allowing for proper control of such confounding effects, as was done in this study. We also note that digestion time decreases along with increasing metabolism, as the sea temperature increases (Nytrø et al., 2014; He and Wurtsbaugh, 1993), further complicating the relationship between salmon lice grazing efficacy by lumpfish and temperature.

5.1.4. Cloud cover

For cloud cover, we found more salmon lice in the stomach contents with clearer weather. This could be because it is easier for the lumpfish to spot the salmon lice when the light conditions are good, as visual perceptiveness of fish might depend on the light level (Cui et al., 1991), and it is known that lumpfish use their vision when hunting food (Paradis et al., 2019). Note that cloud cover was recorded as a subjective assessment.

There might also be potential confounding through recent precipitation and inflow of fresh water, or other potential spatio-temporal effects beyond those accounted for through adjusting for the sea lice abundance.

5.1.5. Lumpfish weight

It is well known that heavier lumpfish have a lower salmon lice grazing efficacy than smaller lumpfish (Imsland et al., 2014b, 2016b; Eliasen et al., 2018; Imsland et al., 2021; Engebretsen and Aldrin, 2020). As we had a large sample of lumpfish, we were able to precisely estimate the continuous relationship between lumpfish weight and salmon lice in the stomach contents. Interestingly, we found an optimal weight of approximately 40 g, where lumpfish below and above 40 g contained fewer salmon lice. While the decreasing effect for large lumpfish is well known, the increase for lower weights has not previously been identified. Hence, due to a flexible model effect and a large number of observations, we are able to contribute with new insight into the relationship between lumpfish weight and sea lice grazing. Note that we do not know whether sea lice grazing decreases for heavier lumpfish due to decreased feeding on salmon lice, or if lumpfish who feed on salmon lice tend to grow less. The prevalence of salmonid feed in the stomach contents, however, has been found to increase with size in lumpfish (Eliasen et al., 2018), which may imply increasing growth and preference for such feed. The reason for the apparent low grazing efficacy at lumpfish weights lower than 40 g is unknown. Gape size limitation seems unlikely to be the cause of such a shift, as juvenile lumpfish can capture prey up to half of their own size (Ingólfsson and Kristjánsson, 2002). Behavioural constraints or physical constraints such as swimming limitations may nonetheless hypothetically limit small individuals from grazing effectively on the salmonid hosts.

5.1.6. Lumpfish density

We found no association between lumpfish density and the number of salmon lice per lumpfish. This is not surprising, as the amount of lumpfish should not matter for the salmon lice grazing by individual lumpfish, unless there are not enough salmon lice for all the lumpfish, inducing a competition effect. However, such a competition effect should show up as a decrease in salmon lice per lumpfish for large values of lumpfish density, and we did not find such a decreasing effect in our analysis (on the contrary, our tendency was slightly increasing). Note that we model the number of salmon lice per lumpfish, and hence the implied total delousing effect in the sea cage will increase with the number of lumpfish in the sea cage. Note also that the lumpfish density is usually a noisy variable, since it is hard to keep track of the exact numbers of lumpfish during production.

5.1.7. Lumpfish condition

We found a positive relationship between condition factor and the numbers of salmon lice in the stomach contents of lumpfish. This suggests that it is important to maintain good husbandry and prevent starvation in the cleaner fish. The actual magnitude of the condition factor effect, however, may be confounded by the time since the lumpfish were released into sea cages or whether the lumpfish feed on salmon pellets. Nevertheless, the positive effect of lumpfish condition agrees with anecdotal experience from fish farming pointing to the importance of keeping a sound husbandry to achieve the wanted delousing effect. To our knowledge, there are no other studies on the relationship between lice grazing and condition.

5.2. Overall salmon lice content

In total, we found that 3.1% of the lumpfish contained salmon lice. This is a lower proportion than the numbers previously reported in the literature. Imsland et al. (2015) found that between 13 and 38% of the sampled lumpfish contained sea lice, while the corresponding proportion in Imsland et al. (2014a) was 10–28% and 13.5% in Eliasen et al. (2018). One reason for the discrepancy could be that since our data are obtained during production, the overall salmon lice abundance is low in our setting, in particular since lumpfish are often used from the start of production when there are few salmon lice in the sea cages. Another possible explanation for these large differences may relate to the sizes of the cages in the studies. The experiments reported in Imsland et al. (2015) and Imsland et al. (2014a) were conducted in small scale net pens (5 × 5 × 5 m), whereas the present data on lumpfish stomach contents are derived from full scale commercial salmon farming cages. This explanation does however not apply to the study by Eliasen et al. (2018), but a reason for this discrepancy may be the substantially higher threshold levels of salmon lice in the Faroese regulations compared to the Norwegian regulations (Kragesteen et al., 2019). Note also that both Eliasen et al. (2018) and Imsland et al. (2014a) include both *Caligus elongatus* and *Lepeophtheirus salmonis* in their definition of sea lice, while we only consider the latter type of sea lice. Imsland et al. (2016b) found a lower proportion of lumpfish containing salmon lice, varying from 0 to 25% in the samples, considering all stages of both *Caligus elongatus* and *Lepeophtheirus salmonis*. The authors speculate that this was due to low overall abundances of salmon lice. Note that even though we only consider salmon lice (*Lepeophtheirus salmonis*) in this study, misclassifications may occur, as it might be difficult to separate between *Caligus elongatus* and *Lepeophtheirus salmonis*. Note also that while there are no missing counts of salmon lice in our data, 6% of the counts of *Caligus elongatus* were missing, which could be due to no *Caligus elongatus*, no registration of *Caligus elongatus*, or that the *Caligus elongatus* were counted together with *Lepeophtheirus salmonis*. If the latter occurred, it could be that the proportion of lumpfish containing salmon lice in reality was slightly lower. The proportion of lumpfish containing *Caligus elongatus* and/or *Lepeophtheirus salmonis* in our data was 3.7%, with an average of 0.25 sea lice per lumpfish (standard deviation 3.6, range 0 to 218). See the supplementary material section S4.1 for a histogram of *Caligus elongatus* in the stomach contents.

5.3. Delousing efficacy

To relate the contents of salmon lice in lumpfish stomachs to delousing effects, we need to know the time from ingestion to either lice are not identifiable in the stomach contents or identifiable lice are evacuated from the stomachs. We have not found such data for lumpfish in the literature, but digestion and evacuation rates in fish are in general dependent on the composition and size of the prey items and temperature (He and Wurtsbaugh, 1993; Amundsen and Sánchez-Hernández, 2019). Nevertheless, if we assume that identifiable salmon lice are retained in stomach samples for 24 h, the present model predictions would imply that 9.5% of the population of salmon lice in a cage would be consumed every day, given a lumpfish density of 10%, lumpfish of 40 g, and an abundance of 0.1 salmon lice per salmonid. If the lumpfish were less efficient at 100 g, the comparable percentage would be 5.1%. At an abundance of 1 salmon louse per salmonid and lumpfish of 40 g, the comparable percentage would be 1.9%. The extent to which these percentages control salmon lice in the cages, however, will ultimately depend on the rates of transmission of salmon lice to the salmonids in the cages and the recruitment rates of the salmon lice within the farms. Note that the number of salmon lice per lumpfish includes all stages of salmon lice, while the salmon lice abundance does not include chalimus. Hence, the proportion of salmon lice consumed per day per lumpfish is likely lower. Unfortunately, we cannot quantify this effect, as we do not know the proportion of the stomach contents which could be attributed to chalimus. However, it has been suggested that lumpfish have a preference for adult female salmon lice (Imsland et al., 2014a; Imsland and Reynolds, 2022).

Cleaner fish may in theory be deployed either already at low lice abundance on the salmonids to control parasite population growth, or at high lice abundance as a delousing treatment. Our results support that lumpfish are more efficient when deployed already at low lice abundance, as the estimated proportion of salmon lice eaten per day is larger when there are few salmon lice present. Lumpfish seem to have a low maximal cleaning rate, and hence seem to be inappropriate as a delousing method during a severe outbreak.

5.4. Limitations

Our study is subject to limitations. As this is an observational study and not a randomised controlled study, there might be several confounding variables. Many of the variables are for example likely confounded with time since deployment, like lumpfish weight and condition factor, salmonid weight, and salmon lice infestation levels. Different operating conditions and salmon lice infestation levels may also lead to different use of lumpfish. However, as our samples are obtained under production, they represent realistic, large-scale operating conditions.

We had to filter out some of the observations due to missing and biologically implausible values. Though we have tried to be as thorough as possible, there might still be some wrong values in the data, as these have been manually recorded. Similarly, there might be observations that we have filtered out that were correctly reported. Note however that we did not filter out observations based on the salmon lice content in the stomachs, and we thus do not expect the filtering to have any qualitative effect on the results.

5.5. Future work

Though we did find an effect of condition factor on the expected number of salmon lice per lumpfish, more research is needed into the relationship between lumpfish welfare and salmon lice grazing efficacy. To be able to provide guidelines for best practice to advice the fish farmers, it is important to gather systematic information on different variables relating to the use, husbandry, and welfare of lumpfish in the fish farms.

Systematic data collection and analysis are thus needed in order to be able to give concrete advice on intervenable factors that could potentially result in both good fish welfare and more efficient delousing. This is particularly important as there is a tendency for premature industrial adoption of new technology running ahead of scientifically sound evidence and documentation, like adoption of lumpfish for delousing. There are also other factors which may affect salmon lice grazing efficacy of lumpfish, which would be interesting to include in future studies. Some suggestions for such factors are velocity, salinity, turbidity, wave exposure, lice control technologies like skirts and snorkel cages, other lice control treatments (particularly grazing efficacy post treatment), exposure to lice-infested salmonids or live feeds prior to deployment, and the availability of alternative food sources for the lumpfish (Eliasen et al., 2018; Overton et al., 2020; Gentry et al., 2020; Hvas et al., 2021).

We did not find an effect of sea temperature on the numbers of salmon lice per lumpfish, contrary to the experience in the industry. Hence, proper experiments on salmon lice grazing by lumpfish at different sea temperatures are needed in order to establish how salmon lice grazing efficacy by lumpfish depends on sea temperature.

In order to translate from salmon lice per lumpfish in the stomach contents to delousing effects, reliable estimates of digestion times for lumpfish are needed. It is also necessary to understand how the digestion times depend on sea temperature. Moreover, to compare delousing efficacy of different cleaner fish species based on stomach contents, we need to know the species-specific grazing rate and digestion times. Hence, this is an important topic for future work, as assessing the delousing effect of lumpfish (and other cleaner fish species) in realistic production settings is crucial for justifying the massive use of cleaner fish in salmonid aquaculture (Overton et al., 2020; Barrett et al., 2020). With reliable estimates of delousing efficacy, these can be used in epidemiological salmon lice infestation models (e.g. Aldrin et al. (2017, 2019)) to simulate the effect of various cleaner fish strategies, e.g. effects of different lumpfish stocking densities.

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CRediT authorship contribution statement

Solveig Engebretsen: Formal analysis, Investigation, Methodology, Conceptualization, Visualization, Writing – original draft, Writing – review & editing. **Magne Aldrin:** Formal analysis, Investigation, Methodology, Conceptualization, Visualization, Writing – original draft, Writing – review & editing. **Lars Qviller:** Formal analysis, Investigation, Methodology, Conceptualization, Writing – review & editing. **Leif Christian Stige:** Formal analysis, Investigation, Methodology, Conceptualization, Writing – review & editing. **Trond Rafoss:** Data curation, Conceptualization, Writing – original draft, Writing – review & editing. **Ole Roald Danielsen:** Data curation, Conceptualization, Writing – review & editing. **Andreas Lindhom:** Data curation, Conceptualization, Writing – review & editing. **Peder A. Jansen:** Formal analysis, Investigation, Methodology, Conceptualization, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Andreas Lindhom reports a relationship with Norsk Oppdrettsservice AS that includes: employment and equity or stocks. Ole Roald Danielsen reports a relationship with Norsk Oppdrettsservice AS that includes: employment. Trond Rafoss reports a relationship with Landbasert Akvakultur Norge AS that includes: equity or stocks.

Data availability

The authors do not have permission to share data.

Appendix A. Supplementary data

Supplementary material to this article can be found online at https://doi.org/10.1016/j.aquaculture.2022.738967.

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