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DEVELOPMENT AND DISPERSAL OF SALMON LICE (*LEPEOPHTHEIRUS SALMONIS* KRØYER 1837) IN COMMERCIAL SALMON FARMING LOCALITIES

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Doctoral thesis

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Abstract

The development and dispersal of salmon lice (*Lepeophtheirus salmonis*) were studied in an intensive aquaculture production site in central Norway, practicing coordinated production cycles. The development of salmon lice on salmon in the localities were studied through three production cycles (2013-2018) by examining count data from the salmon farms themselves. Salmon lice was a more prominent problem the second year of the production cycle. However, in one of the production cycles, the numbers of adult female lice increased and remained at a similarly high numbers from the first summer. The area also showed a change from reliance on medical treatments to a higher proportion of mechanical treatments against salmon lice during the study period.

Possible hindrances of the dispersal of planktonic stages of salmon lice by biofouling on cage-nets or by lice skirts were studied through the last production cycle by investigating the densities of planktonic sea lice on the inside and outside of cages. For cages without lice skirts, the densities of planktonic sea lice were found to positively correlate with temperature the first and second year, and also with the abundance of adult female lice on farmed salmon during the second year of the production cycle. This pattern was similar for salmon cages equipped with lice skirts, except for the correlation with temperature, which was not significant the second year. There were more planktonic lice in periods with a high abundance of parasitic sea lice on the farmed salmon. Neither biofouling on the cage-net nor the presence of a lice skirt seemed to hinder the dispersion of the planktonic stages out of the salmon cages.

No evidence was found for sea lice utilising biofouling as a microhabitat, and *in situ* net cleaning did not affect the densities of planktonic sea lice. During fallowing, no planktonic lice of salmon lice or *Caligus elongatus* were found, and synchronised fallowing in this area was able to curb an escalating salmon lice situation. We also found evidence suggesting that stocking cleaner fish at 4% of salmon numbers or more can delay the time before a locality reaches 0.1 adult female lice per salmon.

Abstract in Norwegian

Utviklingen og spredning av lakselus (*Lepeophtheirus salmonis*) ble studert i et område i Midt-Norge, Frøya, med intensiv lakseproduksjon, og koordinerte produksjonssykluser. Utviklingen av lakselus på laksen ble studert gjennom tre produksjonssykluser (2013-2018) ved å undersøke telledata fra oppdretterne selv. Lakselus var et større problem i andre året av produksjonssyklusen. I en av produksjonssyklusene økte antallet voksne hunnlus allerede første sommeren og holdt seg på samme nivå resten av produksjonssyklusen. Det var et skifte i typen avlusninger som ble brukt, fra medisinske til en overvekt av mekaniske i løpet av studieperioden.

Tettheter av de planktoniske stadiene av lus, gjennom den siste produksjonssyklusen, og mulige hindre for spredning, som begroing på nøter eller luseskjørt, ble studert ved å undersøke tetthetene av planktoniske lus på innsiden og utsiden av merder. For merder uten luseskjørt ble det funnet ut at tetthetene av planktoniske lus korrelerte positivt med temperaturen første og andre året i produksjonssyklusen, men også med andelen voksne hunnlus på laksen andre året. Merder med luseskjørt fulgte de samme trendene, men korrelasjonen med temperatur var ikke signifikant andre året. Det var mer planktoniske lus når det var høyere andel av lus på

laksen. Verken begroing på nøtene eller bruken av luseskjørt så ut til å hindre spredning av luselarver ut av merden.

Det ble ikke funnet noen indikasjoner på at lakselus kan bruke begroing som et mikrohabitat, og vasking av nøter forandret ikke tetthetene av planktoniske lus inne i merden. I løpet av brakkleggingsperioden ble det ikke funnet planktoniske lus av verken lakselus eller skottelus (*Caligus elongatus*), og en synkronisert brakklegging i dette området var i stand til å dempe en eskalerende lusesituasjon. Det ble funnet indikasjoner som tilsier at innblanding av rensefisk over 4% kan forlenge tiden før et anlegg når 0,1 voksne hunnlus per laks.

Contents

List of papers

Paper I:

Jevne, L. S., & Reitan, K. I. (2019). How are the salmon lice (*Lepeophtheirus salmonis* Krøyer, 1837) in Atlantic salmon farming affected by different control efforts: A case study of an intensive production area with coordinated production cycles and changing delousing practices in 2013-2018. *Journal of Fish Diseases, 42*(11), 1573-1586. doi:10.1111/jfd.13080

Paper II:

Jevne, L. S., Øvrelid, M. S., Hagemann, A., Bloecher, N., Steinhovden, K. B., Båtnes, A. S., Olsen, Y., Reitan, K. I. (2020). Biofouling on salmon pen nets and cleaner fish shelters does not harbour planktonic stages of sea lice. *Submitted to a peer reviewed journal.*

Paper III:

Jevne, L. S., Guttu, M., Båtnes, A. S., Olsen, Y., Reitan, K. I. (2020). Planktonic sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) densities at a commercial Atlantic salmon (*Salmo salar*) farms in Norway, through a production cycle. *To be submitted to Aquaculture*

Contributions

Paper I: LSJ planned and carried out the data collection, analysed all data and did the main part of writing the manuscript. KIR participated in planning and contributed to writing.

Paper II: LSJ planned and carried out the fieldwork of experiment B and C, analysed a large part of the plankton samples, did all data treatment and the main part of writing the manuscript. AH and KBS contributed to fieldwork, data analysis and writing of experiment A. MSØ participated in the fieldwork, analysis of samples and the writing process of Experiment B. ASB and NB contributed to planning, analysis of samples and wiring. KIR and YO acquired funding and participated in the planning and writing process.

Paper III: LSJ planned and carried out the fieldwork, analysed a large part of the plankton samples, performed all data treatment and the main part of writing the manuscript. MG and ASB participated to the fieldwork and contributed to the data treatment. YO and KIR acquired funding and participated in the planning and writing process.

Abbreviations

Abbreviation	Definition
95%CI	95% confidence interval
BCa 95% CI	Bias-correlated and accelerated bootstrap (iterations = 2000) 95% confidence intervals
EIP	External infection pressure
Inside-samples	Samples taken on the inside of salmon cages
OR	Odds ratio
Outside-samples	Samples taken on the outside of salmon cages
SD	Standard deviation

Introduction
Salmon lice

Aquaculture is currently the fastest growing food production sector in the world (FAO 2016). Production of Atlantic salmon (*Salmo salar* Linnaeus, 1758) only accounts for 4% of the world's global fish production (by weight, FAO 2018), but in Norway it is the main aquaculture species (95% by tonnage in 2018, Baklien & Steinset 2019). The high value of farmed salmon, along with species captured by fisheries, makes Norway the world's second largest exporter of fish and fish products, after China (FAO 2018). Regarding the production of Atlantic salmon, Norway is the largest producer (51% of production in 2010, Asche et al. 2013), and there is a political will for continued expansion of the aquaculture sector, given sustainable production. One of the biggest bottlenecks to an expansion in the production of Atlantic salmon in Norway is the parasitic salmon louse (*Lepeophtheirus salmonis* Krøyer, 1837), a small crustacean with major consequences (Vollset et al. 2018).

The salmon louse is a salmonid specialist parasite, preferring host species belonging to the three genera *Salmo*, *Salvelinus* and *Oncorhynchus* (Wootten et al. 1982). In 2016, the control and handling of salmon louse was estimated to cost the Norwegian industry 5 billion NOK (~ 54 million USD, Iversen et al. 2017). Economics aside, salmon lice also poses a threat to salmon mortality and fish welfare for farmed and wild fish (Grimnes & Jakobsen 1996, Bowers et al. 2000, Torrissen et al. 2013, Vollset et al. 2018).

A closer look at the life cycle of this parasite is needed to understand the complex relationship between this parasite and its host. Salmon lice hatch

from egg strings attached to the adult female (Schram 2000). It then develops through three planktonic stages before the salmon louse is ready to settle on a new host, with each of these stages separated by moulting (change of their exoskeleton, Johnson & Albright 1991a, Hamre et al. 2013). The planktonic stages are the nauplius stages (I and II) and the copepodid stage. During the planktonic part of their life, they are lecithotrophic, depending on the energy stored in the egg, and they mostly drift with the currents (Schram 1993, Johannessen 2011). They have an innate swimming capability for vertical migration (Heuch et al. 1995), making them able to maintain their vertical position in the water column. However, large scale movements are dependent on seawater currents (Brooker et al. 2018), where they can be dispersed for long distances (Samsing et al. 2017).

In the search of a host, the copepodid stages of sea lice are affected by a range of environmental factors including salinity, temperature, light, chemicals, water mixing, pressure and water flow / vibration (Mackas et al. 1985, Brooker et al. 2018 and references therein, Bui et al. 2020). The copepodids avoid water masses with salinity below 27 ppt (Bricknell et al. 2006), and both copepodids and nauplii of *L. salmonis* have been shown to aggregate just below haloclines (Crosbie et al. 2019). Nauplii are more common in the upper parts of the water column (Gravil 1996, á Norði et al. 2016). Crosbie et al. (2020) showed that the nauplii are also affected by thermoclines, and tend to aggregate in surface layers if temperatures are < 10°C, but aggregate at the thermocline if the upper layer is > 12°C. The vertical distribution of copepodids were not affected by the temperature gradient.

If copepodids manage to find a host before their energy has run out, they will attempt to settle on the host. The settlement success is affected by the age of the copepodid (Gravil 1996), the seawater current speed, the swimming speed of the host (Samsing et al. 2015), salinity and temperature (Tucker et al. 2000, Samsing et al. 2016).

If the copepodid settles successfully, it will use its antennae for initial attachment. After the initial settlement, the copepodid starts feeding and attaches more firmly to the host, preferring places like the fins or other protected areas (Bron et al. 1991). It then starts moulting into the chalimus stage (Brooker et al. 2018). During the chalimus stages (I and II), salmon lice are stationary while eating the epidermis and mucus (White 1942). After moulting two more times, salmon lice become mobile and can move around on the surface of the salmon. The mobile stages are the preadult (I and II) and adult stages (Johnson & Albright 1991a). The appetite of salmon lice increases with size, and during the adult female stage, lice can also consume blood (Brandal et al. 1976). Salmon lice have sexual dimorphism, where the adult female (8-11 mm, maximum recorded length 18.2 mm) is larger than the adult male (5-6 mm, Wilson 1905, White 1942, Johnson & Albright 1991a, Schram 1993).

The development time of salmon lice is highly dependent on temperature, with higher temperatures giving shorter development times (Johnson & Albright 1991b). The generation time from egg to adult for *L. salmonis* is estimated to be 40 and 52 days for the male and the female, respectively, at 10°C. Stien et al. (2005) showed that the minimum development time (D) with increasing water temperature could be described by Belehrádek's

function: $D = a(T - \alpha)^b$, where T is temperature (°C) and a, α and b are fitted parameters (Aksnes et al. 1997, Stien et al. 2005).

The fecundity of adult salmon lice is affected by environmental factors such as temperature, photoperiod and salinity, but also by body size and reproductive age (Ritchie et al. 1993, Heuch et al. 2000, Samsing et al. 2016). The mean number of eggs per string increases after the first pair of egg strings (152 ± 45 eggs string^{-1} $\pm$ SD), and is fairly constant during the subsequent egg strings (285 eggs string^{-1}), although the range is broad (55 to 704 eggs string^{-1}). The maximum number of successive pairs of egg strings during a louse's lifetime has been recorded as 11 pairs (Heuch et al. 2000). Both temperature and salinity also affect hatching success with a lower hatching success at lower temperatures (28% at 3°C, >80% at 5-20°C. Samsing et al. 2016), and lower daily hatching rates at lower salinities (Gravil 1996).

The *Caligidae* contains many species of sea lice (559 species, Ahyong et al. 2011), but in the northern Atlantic Ocean there are two species that infect farmed salmon; the above-mentioned salmon louse (*L. salmonis)* and *Caligus elongatus* Nordman, 1832. These two species are called sea lice in this thesis. The term salmon lice will be reserved for only *L. salmonis. C. elongatus* is smaller (5.4-5.7 mm) than *L. salmonis* (Piasecki 1996). The life cycle follows the same distribution in both species, with the exceptions that *C. elongatus* has four chalimus stages and no preadult stage. The minimum generation time of *C. elongatus* is 43.3 days at 10°C (Piasecki & MacKinnon 1995).

In contrast to salmon lice, *C. elongatus* is a generalist parasite able to infect over 80 different host species (Kabata 1992), and in Norwegian waters it

seems to be most frequently found on lumpfish (*Cyclopterus lumpus* Linnaeus, 1758) and codfish (Gadidae sp., Heuch et al. 2007). *C. elongatus* is currently not regulated in Norway; however, there is an impression that it might irritate salmon more than salmon lice (leading to greater jumping activity). It has been a problem in the northern part of Norway, and in more recent years also further south in Norway (Hemmingsen et al. 2020).

Management

Salmon lice infestations have been a problem for the salmon aquaculture in Norway from its beginning. In 1996, recommendations from a national committee made the groundwork for the National Action plan against Lice on Salmonids (Heuch et al. 2005). Monitoring of lice and, at what louse limits intervention had to be undertaken, came into operation in 1998. Then, the first limit was set to a mean of 2 adult female lice per salmon in the spring. In 2000, the new limit was set to a mean of 0.5 adult female lice per salmon from January to May. Higher levels of lice were permitted during the late summer and autumn (Heuch & Mo 2001). Today, the legal upper lice limit in Norway is set to a mean of 0.2 adult female lice per salmon, for six weeks in the spring (weeks 16-21 for southern Norway up to Nord-Trøndelag and weeks 21-26 for areas further north), and 0.5 adult female lice per salmon during the rest of the year (Forskrift om lakselusbekjempelse 2020, February 04). Table 1 gives an overview of the lice limits in some other salmon producing countries. Lice limits regulate the mean lice per salmon, but do not take into account any density-dependent factors, like the total number of adult lice in a locality or

in an area. This was pointed out in 2001 (Heuch & Mo 2001); however, density-dependent factors were not included in Norway's management plan until 2017, through the 'traffic light system'. The traffic light system

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Table 1 Legal limits of salmon lice per salmon requiring intervention, or other management guidelines, in different countries, AF: adult female lice

Country	Spring	Rest of the year	Source
Ireland	(March-May) 0.3-0.5 egg-bearing lice	2.0 egg-bearing lice	(Jackson 2011)
Scotland legal limit (good practice)	(1st of February to 30th of June) 8 AF (0.5 AF)	(1st of July to 31st of January) 8 AF (1.0 AF)	(Anon 2015, Marine Scotland 2019)
Faroe Islands	-	1.5 AF (after 2017, 2009-2017: 2 AF)	(Kragesteen et al. 2019)
Norway	(week 16-21, or 21-26 for the south and northern part of Norway) 0.2 AF	0.5 AF	(Forskrift om lakselusbekjempelse 2020, February 04)
Canada British Columbia	(January-February) Farms must take measures to reduce lice levels (March-June) Three mobile lice limit	Three mobile lice require increased monitoring, but treatment is not required	(DFO 2014) (DFO 2019)

regulates salmon aquaculture production volumes, in Norway's thirteen production areas, based on the effect that salmon lice produced on salmon

farms in that area, have on the wild populations of salmon in the same area (Vollset et al. 2018).

Chemotherapeutants have been the dominant method for delousing salmon and are administered through either bath treatments (available from 1974 in Norway) or oral treatments (available from 1996 in Norway; Poppe 1999, Burridge et al. 2010). During the early 2000s, delousing of salmon was relatively effective and the problem with salmon lice was thought to be under control (Flathagen 2017). However, the one-sided reliance on chemical treatments lead to that the development of resistance in salmon louse towards commonly used chemotherapeutants (Aaen et al. 2015). During 2012-2017, there was a rapid paradigm shift from the use of chemotherapeutants to non-medical delousing operations (Overton et al. 2018). The non-medical operations include lice flushers, freshwater treatments and thermal treatments (see Table 1, Paper I for an overview of both medical and mechanical lice treatments).

In addition to methods of delousing salmon, multiple other efforts have been made to reduce the sea lice problem. The development of coordinated production zones though the traffic light system is one of them, and other large-scale efforts include synchronised fallowing and synchronised treatments throughout Norway (Forskrift om lakselusbekjempelse 2020, February 07). On a locality scale, there are both technological and biological preventative methods. The technological methods include methods for limiting contact between the salmon and the part of the water column where most of the infective copepodids are expected to be.

This separation can be done by enclosing the upper part of the cage in a skirt or using a snorkel cage (Grøntvedt & Kristoffersen 2015, Stien et al. 2016, Stien et al. 2018). Lasers shooting the salmon lice off the salmon could continuously reduce part of the salmon lice population in a cage (Dumiak 2017) and can be seen as the technological counterpart to cleaner fish.

Cleaner fish are species of fish that are co-cultivated together with salmon with the aim of providing a lice eating service. The most common cleaner fish species used are lumpfish (*Cyclopterus lumpus* Linnaeus, 1758) and different species of wrasse (*Labridae* spp., Overton et al. 2020). Cleaner fish are widely used in Norwegian salmon aquaculture; 49 million were used in 2018, of which 31 million were lumpfish (Norwegian Directorate of Fisheries 2019). There is a welfare concern when using cleaner fish, which is further emphasised by the lack of evidence of cleaning efficiency for some of the wrasse species (Overton et al. 2020).

Studying the planktonic stages of sea lice

The density of the planktonic stages of salmon lice in water masses are low and highly variable, which makes regular counting and therefore also field studies difficult. The mean abundance is usually below 1 ind. m^{-3} in studies investigating densities, but samples with numbers as high as 143 ind. m^{-3} have also been reported (McKibben & Hay 2004). Concentrations of other zooplankton organisms can be much higher (Gallienne et al. 2001), and simply increasing the sample volume to overcome these variations is therefore time-consuming.

Modelling of the distribution of the planktonic salmon louse stages overcomes some of these difficulties when studying these organisms

directly in water masses. Models are today used in Norway's traffic light system (Vollset et al. 2018). Though the models are constantly updated when new knowledge is generated (Skogen et al. 2020), the validation of the model system is done through comparisons with lice counts on salmon held in sentinel cages (Sandvik et al. 2016). There is a lack of information on the dose-response relationship between numbers of planktonic salmon lice and numbers of salmon lice found on the salmon in sentinel cages. Comparing salmon lice counts from sentinel cages with the number of adult female salmon lice on salmon in the area can therefore be challenging (Skogen et al. 2020).

Direct observations of planktonic sea lice in the water masses are scarce and thus the knowledge of the abundance of planktonic salmon lice continues to be an important knowledge gap. Studies of planktonic sea lice have been conducted in Canada (Stucchi et al. 2011, Byrne et al. 2018, Nelson et al. 2018), Scotland (Gravil 1996, McKibben & Hay 2004, Penston et al. 2004, Penston et al. 2008, Penston et al. 2011, Salama et al. 2013, Frenzl 2015), Ireland (Costelloe et al. 1996, Costelloe et al. 1998), the Faroe Islands (Nordi et al. 2015, Nordi et al. 2016) and Norway (Skarðhamar et al. 2019). Densities of planktonic sea lice have been found to be higher in samples taken close to salmon farms than in samples taken further away (Costelloe et al. 1996, Penston et al. 2004, Nelson et al. 2018). Byrne et al. (2018) showed that there was a correlation between the density of planktonic stages of sea lice, found in the water at the farm, and the number of mobile salmon lice on the salmon at the farm. There is apparently also a correlation between the density of copepodids of salmon lice found some distance away from the salmon farm, and the presence of adult female lice on the salmon at the farm (McKibben & Hay 2004).

Earlier studies have also found higher densities of planktonic sea lice on the inside of salmon cages compared to the outside (Costelloe et al. 1996, Gravil 1996), and speculated that the dispersion of planktonic sea lice might be hindered by the net or net biofouling. However, recent studies found no differences in densities inside and outside of the sea cages (Nordi et al. 2016, Nelson et al. 2018).

The present thesis and works therein contribute to filling the knowledge gap about the planktonic stages of salmon lice, by taking a holistic perspective on the salmon lice situation in an intensive salmon aquaculture area, in coastal central Norway. This area practise coordinated production cycles, and Paper I describes the development of salmon lice for the entire are, not as a mean per salmon or locality, but as a total for the area during three consecutive production cycles. Paper II investigated if planktonic salmon lice dispersal out of the cage was limited by the net or biofouling on the net. Paper III investigated the densities of planktonic sea lice during the last production cycle described in Paper I, at three of the commercial salmon farms in the study area.

Aims of the study

The main goal of this thesis was to investigate the development of salmon lice in commercial salmon farming localities, and the dispersal potential of their planktonic stages.

The sub-goals were to i) investigate the development of parasitic salmon lice on salmon for an area, and to link the attached salmon lice on the salmon and the densities of planktonic sea lice in the surrounding water, ii) investigate if the dispersion of planktonic sea lice out of a salmon cage would be affected by biofouling on the cage-net and iii) describe the

presence and dispersal of planktonic salmon lice during the course of a production cycle.

To accomplish this, specific research questions were formulated as listed below:

- How does the salmon lice population develop in an area with coordinated production cycles? (Paper I)
- How did the management of salmon lice change in the study area during the years 2013-2018? (Paper I)
- To what extent do planktonic sea lice utilise biofouling on submerged structures on salmon farms as microhabitats? (Paper II)
- Does the amount of biofouling on salmon cage-nets or the utilisation of a lice skirt create a dispersal barrier for planktonic sea lice? (Paper II)
- Is there a link between the abundance of parasitic sea lice, on the salmon, and the density or prevalence of planktonic sea lice inside or outside of salmon cages? (Paper III)
- What is the background level of planktonic salmon lice during the fallowing period? (Paper III)

Summary of papers

Paper I

How are the salmon lice (*Lepeophtheirus salmonis* Krøyer, 1837) in Atlantic salmon farming affected by different control efforts: A case study of an intensive production area with coordinated production cycles and changing delousing practices in 2013-2018.

Authors: Lone S. Jevne, Kjell I. Reitan

In this paper, we investigated the fluctuations in salmon lice in relation to control efforts on an area basis. Data consisting of weekly numbers of salmon and salmon lice, treatments against salmon lice and number of cleaner fish deployed were gathered from all of the study area's (northern Frøya) 16 salmon farms. These data were used to look for trends for the area as a total by exploratory analysis and survival analysis. The results showed a trend from sole reliance on medical treatments against salmon lice to sole reliance on mechanical treatments from the first to last study year (2013-2018). The study also showed an increase in the use of preventative actions against salmon lice, with an increase from 10 to 50% of salmon cages utilising lice skirts, and an increase in the use of cleaner fish. It also suggests that the timing of when cleaner fish are deployed may have an effect on their effectiveness, as it was found that localities with more than 4% cleaner fish in their cages later had 0.1 adult female salmon lice on their salmon.

Paper II

Biofouling on salmon pen nets and cleaner fish shelters does not harbour planktonic stages of sea lice.

Authors: Lone S. Jevne, Margrete S. Øvrelid, Andreas Hagemann, Nina Bloecher, Kristine B. Steinhovden, Anna S. Båtnes, Yngvar Olsen, Kjell I. Reitan.

In this paper, we investigated the role of biofouling on the cage-net and the utilisation of lice skirts in the dispersal of the planktonic stages of sea lice. The presence of planktonic sea lice was analysed in net pieces collected from the cage-net, after the net pieces had been deployed for five months. This was in order to investigate if biofouling can act as a microhabitat for planktonic sea lice. Possible resuspension of planktonic stages of sea lice after net cleaning were investigated through the collection of plankton samples at different stages in a net cleaning cycle. The possibility of biofouling exerting a shielding effect, in a similar manner as lice skirts, were also investigated. No evidence was found for planktonic stages of sea lice utilising biofouling as a microhabitat. No differences in the densities or prevalence of planktonic sea lice between the inside and the outside of cages without lice skirts was found. A shielding effect was found in one of two cases where lice skirts were utilised around cages. The results of this study therefore suggest that the presence of biofouling had no impact on the planktonic stages of sea lice and that planktonic sea lice do not utilise biofouling as a habitat.

Paper III

Working title: Planktonic sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) densities at a commercial Atlantic salmon (*Salmo salar*) farms in Norway, through a production cycle.

Authors: Lone S. Jevne, Maria Guttu, Anna S. Båtnes, Yngvar Olsen, Kjell I. Reitan.

Manuscript for submission to *Aquaculture*

This paper investigated the density and distribution of planktonic stages of sea lice at three commercial salmon farms for the duration of one production cycle. The aim was to gain knowledge about the link between the number of parasitic lice on the salmon and the densities of planktonic sea lice. Dispersal of planktonic sea lice out of the cage was also investigated. To investigate the background densities of planktonic stages of sea lice in the area, the sampling program continued into the subsequent fallowing period, when no contribution from salmon farms was present.

The results show that planktonic sea lice dispersed out of the cages regardless of the presence of a lice skirt. The densities of planktonic sea lice were highest in periods with high lice loads on the salmon and at higher temperatures. The results suggested a shift in correlations between the first and second year of the production cycle. In the localities without lice skirts, the best correlations were found for densities of planktonic sea lice and temperature, and for densities of planktonic sea lice and the predicted nauplius production on the cage level. For the locality with lice skirts, samples taken from inside the cage showed a correlation for the densities of planktonic lice to both temperature and adult salmon lice on salmon,

although the former was positive and the latter was negative. In the second year, the correlations for the densities of planktonic sea lice and adult female lice on salmon were positive, and the correlation for the density of planktonic sea lice and temperature was no longer significant.

Methods
Plankton sampling

Skarðhamar et al. (2019) studied the copepodid stage of salmon lice in two Norwegian fjords. Their main goal was to compare different sample gear to collect planktonic stages of sea lice. They found the vertical plankton tow to be the most robust and convenient sampling gear, which could sample a high volume of water without being too hampered when the weather conditions were less than optimal.

All the planktonic sea louse samples throughout this thesis were collected with vertical plankton tows. During the earlies study (experiment B, Paper II) a plankton tow with a mesh size of 200 µm was utilised, as recommended by an earlier study in order to reduce clogging of the net (Schram 2004). The later studies in this thesis utilised a plankton tow with a mesh size of 150 µm, which is smaller than the width of all planktonic stages (Schram 2004). In the first study (experiment B, Paper II) the samples were sieved through a 500 µm filter in order to remove coarser material but let the planktonic sea lice through, as their width is < 300 µm. This method was based on what had been done in a study by Costelloe et al. (1996). However, during the subsequent studies, this was not done due to the possibility of planktonic sea lice also being filtered out, as their length can be > 500 µm.

Although direct comparison across studies with different methodology is questionable, the studies in question compared the samples taken on the inside of the cage (inside-samples) with those taken on the outside of the cage (outside-samples). It is the difference between the inside- and outside-

samples that is compared across studies, through comparisons of the odds ratios (OR) for prevalence.

Five different localities were investigated in the studies of this thesis; abbreviations and locality sizes are given in Table 2.

Data treatment and statistics

Measures of planktonic sea louse densities (prevalence and mean intensity *vs.* mean abundance)

Sampling a distribution that gives more zero samples than expected (zero inflation), which also have a variance higher than the arithmetic mean (overdispersion, Murray et al. 2011), can result in a measure of the mean or the median that in many cases is insufficient. In the case of overdispersion without zero samples, the distribution is skewed to the left,

Table 2 Overview of localities where samples were collected in Paper II and Paper III.

Paper	Locality	Municipality	Number of net pens on locality (circumference)
Paper II & III	**NoskirtA**	Frøya	9 (157 m)
Paper II & III	**NoskirtB**	Frøya	7 (157 m)
Paper II	**NoskirtC**	Lurøy	16 (90 m)
Paper II	**Liceskirt10** (10 m deep lice skirts)	Frøya	5 (135 m)
Paper II & III	**Liceskirt7** (7 m deep lice skirts)	Frøya	15 (157 m)

with a heavy tail to the right, meaning that although most samples have small values, there are some that have much higher values than the rest. Taking a mean of this distribution would give a higher mean value than most of the samples had. In such a case, the median would be a better option, as it gives the value of the sample in the middle of the distribution. The median would, however, not give a meaningful measure in a case where many of the samples are zero. Both overdispersion and zero inflation are common in parasitology, as parasites accumulate on some individuals, and many host individuals are without any parasites (Murray et al. 2011).

Both prevalence and mean intensity are commonly used in the description of parasite densities (Rozsa et al. 2000). Prevalence gives the ratio of infested to uninfested hosts of the hosts sampled, and mean intensity gives the mean parasite load on the subset of hosts that are infested. Giving both the prevalence and mean intensity would therefore give information about the number of uninfested hosts (zero samples) and how many parasites there generally were on infested hosts (mean intensity). The distribution of planktonic sea lice is patchy (Sandvik et al. 2016), with a high variation in parasite numbers and where samples with zero individuals are frequent. Expressing the state of planktonic sea lice through the prevalence and mean intensity could give more sensible information about the distribution in the water.

Mean abundance incorporates both the zero samples and the samples with lice into one expression. There are times where the mean abundance can make interpretation of the relationship easier. The development time of salmon lice is highly affected by temperature, with higher temperatures leading to faster development and generation cycles, while colder

temperatures slows development down. At lower temperatures, lower levels of planktonic salmon lice in the samples would therefore be expected than at higher temperatures, given the same abundance of adult female lice in the sample cage.

The prevalence and mean intensity would capture some of this relationship, and we found a dip in prevalence and mean intensity during the colder months, especially for the locality NoskirtA (Figure 4 and Figure 5 in Paper III). Because prevalence is based on presence-absence data, it does not capture the magnitude of change, from Summer (June-November) to Winter (December-May). Mean intensity can capture change in the portion of samples that have planktonic salmon lice, but do not reveal the change in prevalence. Mean abundance will in this case give additional information to mean intensity, because mean abundance is the mean across all samples. Mean abundance will, because of this, be lower than mean intensity in all cases where the prevalence is lower than 100%.

Correlation, partial correlation and semi-partial correlation

The correlation coefficient is the measure expressing how two variables vary together; the most commonly used correlation coefficients are Pearson rho (r), Spearman's rho (r_s) and Kendall's tau (τ). Pearson's r assumes that the variables are normally distributed and that they have a linear relationship. Spearman's r_s converts the measurements to rank before checking the correlation, and does not assume a normal or linear relationship, but does assume a monotonically increasing or decreasing relationship. Kendall's τ is in many ways a similar measure to Spearman's r_s, but is better for smaller sample sizes and when there are ties between the variables (Field et al. 2012). Kendall's τ is less commonly used than both Spearman's r_s and Person's r correlation coefficients, but can be

transformed into Spearman's r_s, or Person's r for easier interpretation of the effect size (Gibbons 1976, Gilpin 1993).

A high correlation is not the same as causation and must be carefully interpreted. There can, for example, be a covariable, called a confounding variable, affecting one or both of the studied variables. Partial and semi-partial correlation tries to account for this. If there are three variables, e.g. density of planktonic sea lice (Y), abundance of adult female lice on the salmon (X) and sea temperature (Z), and if X and Y are independent of Z, all three correlation coefficients will be equal (normal, partial and semi-partial). If Z only affects Y, the normal correlation coefficient will be different, but both the partial and the semi-partial correlation coefficient will be the same. However, if Z affects both X and Y, all correlation coefficients will be different. It is important to note that, even when accounting for Z, correlation does still not equal causation, but at least one confounding factor has been accounted for (Field et al. 2012).

Results and discussion

How salmon lice are managed is changing quickly. New knowledge of how the different management strategies affect salmon lice are sometimes obscured by the large differences in environment and management practices between different aquaculture areas and sites. This is perhaps best illustrated by the different effects the same management strategies can have when tested under different conditions. Lice skirts are in some cases shown to have a large shielding effect (80% reduction in lice infection; Stien et al. 2018), but other studies have found a lower effect (18% reduction in lice attachment; Grøntvedt & Kristoffersen 2015). Different management strategies can affect each other's efficiency, making the situation further complicated. One example is the reduced consumption of lice by the cleaner fish corkwing wrasse in the presence of lice skirts (Gentry et al. 2020).

L. salmonis and *C. elongatus*

In the effort to find new control methods, another factor to consider is the presence of two different species of sea lice, *L. salmonis* and *C. elongatus*. While DNA analysis can distinguish between these species (McBeath et al. 2006), their nauplii stages are difficult to identify when observed through a stereomicroscope. The only reliable characterisation is the different pigmentation, which quickly disappears when fixed in either ethanol or formalin (Schram 2004, Danielsen 2014). The two species are therefore sometimes grouped together as sea louse larvae (Nauplius 1&2 and copepodid stage) during counting and further analysis (Byrne et al. 2018, Paper II and Paper III). This treatment mask differences between the species and may lead to further problems.

The older stages are easier to identify to species, and the oldest stages can be separated by eye. While legal louse limits in Norway ensure that salmon lice are counted regularly, numbers of *C. elongatus* are not regulated in Norway. In the cases where *C. elongatus* are counted, they are usually grouped into one age category, in contrast to the three reported categories required for salmon lice: sessile, mobile and adult female. The reported numbers of salmon lice can be viewed and downloaded from databases such as BarentsWatch (BarentsWatch 2019, November 26), but because numbers are reported as averages for the locality, the true size of the salmon lice population is concealed. When a locality reports 0.1 adult female lice per salmon, the total number of lice can be very different depending on the number of salmon at that locality. The same can be said for an area with a different number of salmon localities.

In Paper I, we calculated the total numbers of salmon lice for the area Northern-Frøya, central Norway, not the average per locality. All lice categories were significantly higher in the second year of the production cycles (adult female lice: $\chi^2(1) = 785$, $p < 0.001$, mobile lice: $\chi^2(1) = 259$, $p < 0.001$, sessile lice: $\chi^2(1) = 29$, $p < 0.001$), which is in accordance with earlier studies (Jackson et al. 2000, Revie et al. 2002b). In production cycle two, adult female lice quickly increased during the first summer and reached more than 5 million for the area as a total (Figure 1).Despite each locality adhering to the legal limits and delousing when the numbers climbed above 0.5 adult female lice per salmon, the investigation showed that total the number of adult female lice remained above 1.5 million in the area, for the rest of the production cycle. The higher numbers of adult female lice in production cycle two can be a result of several factors. The effectiveness of the treatments could have been lower than optimal for this

production cycle. This was a time when the salmon louse developed resistance to medical treatments and when the mechanical treatments were still relatively new (Aaen et al. 2015, Overton et al. 2018). This is reflected in the change from sole reliance on medical treatments in production cycle one (100%) to mechanical treatments being utilised in a larger proportion in production cycle three (64%).

There was also a significantly ($\chi^2(1) = 2.74$, p < .01) earlier deployment of cleaner fish in production cycle three (6.0 ± 5.9 weeks after salmon deployment) compared to production cycles one and two (16 ± 4.5 and 17.5 ± 7.4 weeks after salmon deployment respectively). Lumpfish have been shown to exhibit stress responses during their first encounter with Atlantic salmon (Staven et al. 2019), and earlier deployment of lumpfish might give them time to acclimate before the salmon lice arrive. We also found evidence for a delaying effect of cleaner fish on the time until salmon reached 0.1 adult female lice when cleaner fish were stocked at ≥4% of the salmon in the cages, compared to localities which stocked <4% cleaner fish. The hazard ratio between cleaner fish groups (< or ≥4% stocked cleaner fish), found in a multivariate Cox proportional hazard regression model, adjusted for production cycle and the presence of adult female lice in the area the week before, was 0.38 (95% confidence interval: 0.18-0.84, p < 0.05). This can be translated to a 62% reduction in the chance that a locality stocked with 4% cleaner fish or more would reach 0.1 adult female lice per salmon from one week to another, when compared to a locality stocked with less than 4% cleaner fish (Paper I).
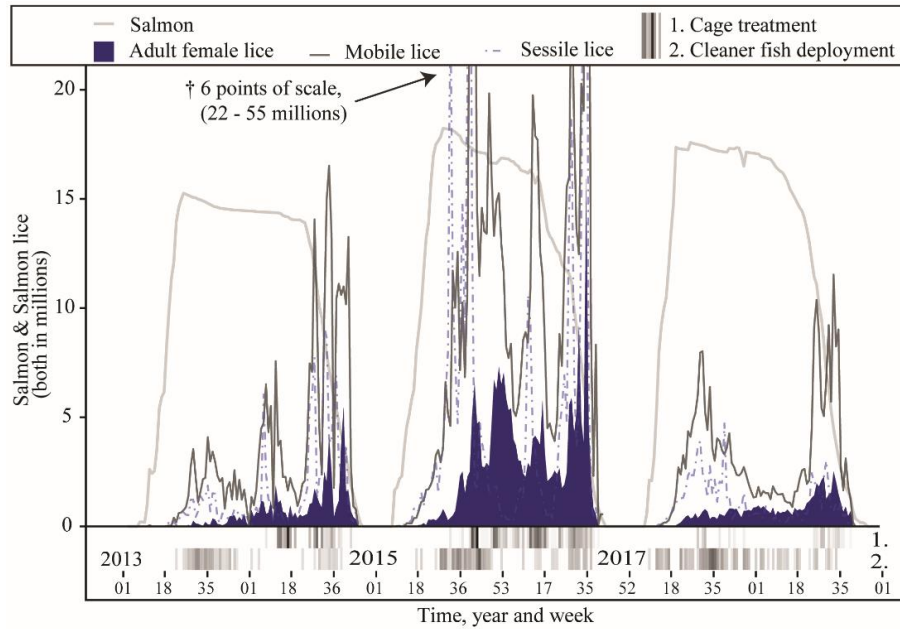
Figure 1 Number of salmon (*S. salar*) and number of salmon lice (*L. salmonis*) for the study area during the three production cycles 2013-2014, 2015-2016 and 2017-2018. The y-axis shows number of salmon and salmon lice in the area. Salmon (grey line), sessile salmon lice (dotted line), mobile salmon lice (dark grey line) and adult female salmon lice (dark blue area). The bands underneath the graph shows the number of cages treated for salmon lice (1.), where darker colours mean that a higher number of cages were treated. Black equals 60 treated cages. The second band shows the distribution of cleaner fish deployment (2.), with darker colours indicating that more cleaner fish were deployed that week. †The six points above the scale are here given in millions for each year and week; sessile lice: 22, 33, 29 and 40 million in year-week 2015-32, 2015-40, 2016-34, 2016-35, respectively. Mobile lice: 22 and 55 million in year-week 2015-40 and 2016-35 (Paper I).

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C. elongatus was not quantified in Paper I, but the numbers can be found for three of the localities in the same area for the last production cycle in Paper III. The numbers of *C. elongatus* on salmon were highest in the first year of the production cycle. For the locality with lice skirts, the abundance of *C. elongatus* in the first year was higher than the abundance of salmon lice at the end of the production cycle. The two localities without lice skirts both exhibited a maximum in *C. elongatus* abundance in the first year, but the numbers were lower and surpassed by counts of salmon lice at the end of the production cycle.

The emergence of *C. elongatus* is reported to be a larger problem in northern Norway compared to central Norway (Hemmingsen et al. 2020). However, experiences from areas further south in Norway during recent years suggests that a preconditionary approach would call for more attention on *C. elongatus*. Numbers of *C. elongatus* should likely be reported similar to the practice for salmon lice, with separate categories for adult female *C. elongatus* and, if possible, with some or all different age groups. Implemented management practices could then be compared for the two species across localities, because the effects might differ between the species.

Stien et al. (2018) speculated that lice skirts were not expected to have any substantial effect on *C. elongatus* because *C. elongatus* have a wider range of potential hosts, and that its larvae might not have evolved the same tendency to aggregate in the surface water (á Norði et al. 2015). The higher abundance of parasitic *C. elongatus* at the locality with lice skirts in Paper III were in accordance with this speculation. Because only one locality with lice skirts was studied, the higher abundance of *C. elongatus* at this locality

could regrettably have been due to other factors. Fallowing is another preventative technique which is expected to have a weak effect against *C. elongatus* (Revie et al. 2002a). The discussion is still ongoing regarding the effects of fallowing on salmon lice.

Fallowing and coordinated production cycles

Fallowing reduces overall mortality rates at salmon farms (Wheatley et al. 1995) and has been used to combat furunculosis (Rae 2002). In Paper III, we found no planktonic salmon lice or *C. elongatus* during the fallowing period. Paper I and other studies showed that the period after a fallowing are often characterised by low levels of salmon lice, and that fallowing can be an effective tool to obtain low numbers of salmon lice at the beginning of a production cycle (Bron et al. 1993, Rae 2002). It is believed that the coordination of fallowing across multiple salmon farms situated in a region, would be most effective in reducing lice levels for an area (Revie et al. 2002a, Arriagada et al. 2017). Fallowing and coordinated fallowing, through coordinated production cycles, could thus be a potential proactive method for controlling salmon lice that does not depend on medicine or chemicals.

Fallowing is based on the principle of temporarily taking away the hosts of the parasite or disease. Because the majority of salmon lice nauplii are believed to be produced in salmon farms, fallowing an area will lower the number of nauplii produced in that area during the fallowing period. However, copepodids from infested wild populations of salmonids, or other still active salmon farming areas, can act as an infection source for newly deployed salmon. Paper I was a case study of an area where coordinated fallowing was practiced. Figure 2 illustrates the predicted production of nauplii in the area during the last two production cycles studied.
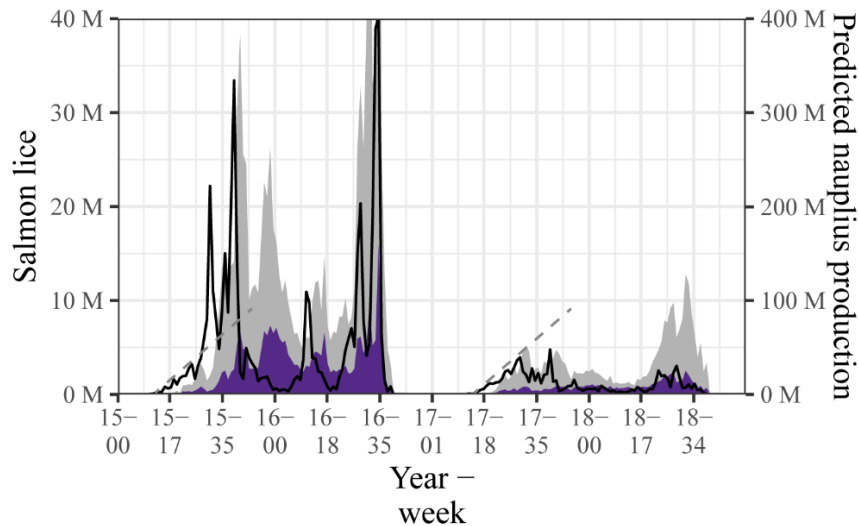
Figure 2 Total salmon lice (*Salmo salar*) numbers and predicted nauplius production for the study area (northern Frøya) during the period 2015-2018. Left axis: number of salmon lice; adult female lice (purple area), sessile (black line). Right axis: predicted nauplius production (grey area). Both for the management area, northern Frøya. M = million. Grey dashed lines are parallel, drawn in as guidelines. Nauplii predictions are based on Equations 1-3 in Stucci et al. (2011), with coefficients suggested by Stien et al. (2005).

Figure 2 shows that the second and third production cycle started similar with regards to sessile and mobile lice. It therefore seems that the fallowing period between production cycles one and two, lasting for 12 weeks, was long enough to give this area a restart in terms of the lice population. During the second production cycle of that study, the salmon lice situation escalated early and continued to remain high until the next fallowing period, despite high treatment intensities. In the case of production cycle

two, coordinated fallowing seemed to be the only thing that was able to stop the galloping lice situation.

It is a vital question if synchronised fallowing can be utilised beyond a last resort in the management of salmon lice. Guarracino et al. (2018) studied the efficiency of synchronised fallowing in two salmon farming areas in Norway, in a fjord (Hardangerfjorden) and in a more open coastal area (Vikna). They found that the external infection pressure (EIP) at the beginning of the production cycle, after an area was fallowed, were high because of a substantial influx of salmon louse larvae from the surrounding areas. A higher EIP is found to be related to a higher number of mobile salmon lice during the first 16 weeks after salmon deployment (Kristoffersen et al. 2014). The Hardangerfjord study area consistently showed the highest EIP values (Guarracino et al. 2018). The authors stated that the current management areas (groups of salmon farms with coordinated production cycle) might be the problem in their study, because salmon lice were thought to be capable of spreading between the management areas that were fallowed and those that were not fallowed. Salmon lice can be transported for long distances, as a model showed that the most common distance a salmon lice was transported was 11 km in the spring and 19 km during the winter (Samsing et al. 2017). Guarracino et al. (2018) concluded that fallowing practises do not work as intended, but also cautioned against combining management areas because of the possible negative consequences of a higher salmon biomass at the end of a synchronised production cycle.

There is evidence of a critical threshold in the stocking density of salmon, below which, without treatment, epidemics of salmon lice occur

infrequently but are more inevitable above the threshold. This threshold value varies with abiotic factors and with regional variation in the connectivity and density of salmon farms (Frazer et al. 2012). However, the quick development of salmon lice in the beginning of both production cycle two and three in Paper I may suggest that the biomass of salmon surpasses this threshold from the start of the production cycle for the study area.

Coordinating production cycles in an area will create a cyclic biomass, low in the beginning and high at the end of the production cycle. An area without coordinated production cycles would show less variation in the biomass with time. Given the same connectivity between farms, in areas with and without coordinated production cycles, it appears that newly deployed salmon in the latter area would experience a higher EIP at the beginning of the production cycle. Assuming that smaller salmon have a lower tolerance for salmon lice (Wagner et al. 2008), and that cleaner fish might need an acclimation period after being introduced to the salmon cages (Staven et al. 2019), a lower lice level in the beginning of a production cycle seems preferable. It therefore seems worth figuring out if coordinated fallowing could work under any scenario.

In order to do so, it is vital to establish how connected the management areas are to other management areas in the vicinity, and to evaluate both the potential positive effects in the beginning of the production cycle and the potential negative effects at the end of the production cycle. The positive effects should include a lower infection pressure during the start of the production cycle, and a reset of the area's internal infection pressure during the fallowing period. If the management area is highly connected

with other management areas, these positive effects may disappear, as found for the Hardangerfjord study (Guarracino et al. 2018). The negative effects are likely to include, among others, a higher lice load at the end of the production cycle, due to the fact that lice numbers on a salmon farm tend to increase with increasing biomass, i.e. towards the end of the production cycle. Fully quantifying and evaluating all effects is a comprehensive task, as they might include effects from other diseases (Rae 2002) and some effects might change as the salmon grow (Overton et al. 2018). It should nonetheless be done, as this would increase our understanding of density-dependent factors in the salmon/salmon lice cycle.

Planktonic sea lice distribution in salmon farming localities

Although studies on planktonic stages of sea lice have received considerable attention in recent years, the present thesis provides, to my knowledge, the first direct quantifications of planktonic sea lice for a whole production cycle in salmon farms in Norway.

Dispersal out of salmon cages

Most of the planktonic sea lice individuals found in Paper II and III were in their nauplius stage (98.5%), comparable to that found in earlier studies (Gravil 1996, Nordi et al. 2016, Byrne et al. 2018, Nelson et al. 2018). The results presented in Paper II and III revealed no differences in the prevalence of planktonic sea lice found in inside-samples and outside-samples from salmon cages with high biofouling ($\geq$ 30% biofouling odds ratio: 0.77, 95% CI: 0.15-3.93, $p > 0.05$), low biofouling ($<$ 30% biofouling odds ratio: 1.53, 95% CI: 0.47-5.10, $p > 0.05$), or cages equipped with a 7 m deep lice skirt (odds ratio 2.02, 95% CI: 0.54-8.08, $p > 0.05$, Figure 3).
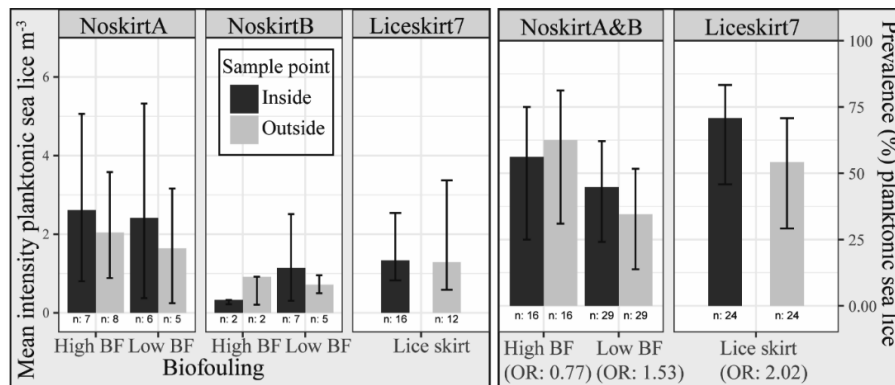
Figure 3 Left: Mean intensity of planktonic sea lice (individuals m^{-3}, mean intensity is based on only those replicates containing at least one sea louse) for samples taken from the inside and outside, of localities either equipped with 7 m deep lice skirt (Liceskirt7), or without lice skirts (NoskirtA and NoskirtB). Right: Prevalence of planktonic sea lice (% of replicates with at least one sea louse) for samples taken from the inside and outside. Odds ratio (OR) for prevalence in samples taken on the inside and outside are marked with * if significant ($p < 0.05$). Both: divided by experiment and site (column panels), and biofouling category (row panels, high BF: biofouling $\geq$ 30%, low BF: biofouling <30%, lice skirt). Total number of replicate net pens in each category is shown by n = x under the bars. Error bars show bias-corrected and accelerated bootstrap (2000) 95% confidence intervals (Paper II).

No difference in the mean intensity of planktonic sea lice m^{-3} was found for these groups (Figure 3, bootstrap two-sample t-test, $p > 0.05$). This suggests that planktonic sea lice disperse out of cages, also in cases when they are equipped with lice skirts or have developed a high degree of biofouling. These results are in agreement with those found in recent years (Nordi et al. 2016, Nelson et al. 2018), though they contrast with earlier

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studies that found higher levels of planktonic sea lice on the inside of cages (Costelloe et al. 1996, Gravil 1996).

A locality with 10 m deep lice skirts was also investigated in Paper II, and for this locality a significantly higher prevalence of planktonic sea lice was found in the inside-samples compared to the outside-samples (odds ratio 17.4, 95% CI 3.6-120.4, p < 0.001). If the mixing depth of water is deeper than the protective depth provided by the lice skirt, mixing of the water masses can occur (personal communications/unpublished data, Jónsdóttir 06 December 2019). No stable pycnoclines were found in the upper 25 m for the three localities studied in Paper III, which suggests that the mixing depth was located deeper. The lack of difference in densities between the inside-samples and outside-samples for the locality equipped with 7 m deep lice skirts (p > 0.05) could therefore be because mixing of the water occurred between the inside and outside of the lice skirt. Biofouling is not uniform with depth (Edwards et al. 2015), and if mixing could occur for the locality equipped with lice skirts, a possible shielding effect from biofouling could also have been obscured by mixing of the water underneath the most biofouled area. For the area studied in Paper II and Paper III, biofouling on the cage-net or lice skirts likely did not exert an adequate shielding effect to prevent the dispersal of planktonic stages of sea lice out of the cage.

In order to investigate if planktonic sea lice utilised biofouling as a microhabitat, net pieces from the cage were analysed for the presence of planktonic sea lice (Paper II). Net pieces were deployed with the salmon cage and were allowed to accumulate biofouling for 5 months. Only one nauplius of sea lice was found on the net pieces. Also, no evidence for a

resuspension of planktonic sea lice was found during *in situ* net cleaning with high pressure washers (before: 4.8, BCa 95% CI 2.1-12.4, after: 1.7, BCa 95% CI 1.2-2.6; bootstrap two-sample t-test = 1.27, p = 0.38). Based on the findings in Paper II, it is unlikely that biofouling is a microhabitat for sea lice.

Planktonic sea lice densities

Samples taken inside the cages in Paper III gave a mean abundance most often lower than 0.4 planktonic sea lice per m^3 seawater (total all localities: 29/42, Liceskirt: 7/14, NoskirtA: 9/14, NoskirtB: 13/14, Paper III). A study from Canada during parts of a production cycle used similar sampling gear inside salmon cages as that used in Paper II and Paper III and reported that planktonic sea lice numbers were related to the number of salmon lice on the salmon (Byrne et al. 2018). The volume of each sample during our study (2.37 ± 0.36 m^{-3} seawater, Paper III) was comparable to the samples of 2.7 ± 0.0 m^{-3} seawater taken by Byrne et al. (2018).

Byrne et al. (2018) generally found a higher mean abundance of planktonic sea lice (≥ 0.4 planktonic sea lice per m^3 seawater, for 8/10 sample months). However, Paper III found higher maximum mean abundance of planktonic sea lice during the months with the highest recorded values (August and September). The highest mean abundance found during our study was 3.5 ± 4.8, 12.4 ± 4.9 and 0.3 ± 0.4 planktonic lice per m^3 seawater, for Liceskirt, NoskirtA and NoskirtB, respectively. The highest values Byrne et al. (2018) found were 1.2 ± 0.6 planktonic lice per m^3, in January. In Paper III, we pooled two plankton tows from 0-7 m into one sample, whereas Byrne et al. (2018) took one sample from 0-18 m. Since sea lice nauplius abundance decreases with depth (Gravil 1996, á Norði et al. 2016), the mean abundance per m^3 seawater between these two sample methods is

therefore not likely to give the same estimates even if they had been taken at the same place and time. In addition, these two studies were conducted in two different countries with different salmon lice limits, and two different oceans that have genetically different *L. salmonis* (Skern-Mauritzen et al. 2014).

Byrne et al. (2018) found a moderately positive correlation between the densities of planktonic sea lice and the number of mobile lice (both *L. salmonis* and *C. elongatus*) on the farmed salmon. In Paper III, we found that there was a reduction in the correlation coefficient when differences in temperature was accounted for with semi-partial correlation. Not accounting for temperature in our calculations would mean that we would have interpreted some of the correlation from temperature as an effect from the tested relationship. We found a moderate correlation between the mean intensity of planktonic sea lice m^{-3} in inside-samples from the Liceskirt7 locality and the number of adult female lice on the salmon in the second year in the production cycle (semi-partial Kendal's tau: 0.43, $p < 0.05$). This was of a similar magnitude as the relationship described by Byrne et al. (2018). For the localities without lice skirts, there was a significant moderate correlation between densities (mean intensity and mean abundance) of planktonic sea lice found in inside-samples and temperature, for both years of the production cycle. For the Liceskirt7 locality, temperature was only significantly correlated with the densities in the first year of the production cycle.

Costelloe et al. (1996) found a large difference in the densities of planktonic stages of sea lice in relation to the tides, with low numbers at low tide and high numbers at high tide. When the densities of planktonic

sea lice found in Paper III were related to the time since high water, no relationship was found (data not shown), but the study was not designed to capture such a relationship.

Because planktonic sea lice are not uniformly dispersed with depth (Gravil 1996, Nordi et al. 2016), sampling gear that samples different subsets of the water column is likely to give different densities. For example, horizontal plankton tows sample water masses at one depth over a large area, while vertical plankton tows sample parts of the water column at one horizontal sampling point (Skarðhamar et al. 2019).

Direct comparison between planktonic sea lice densities must be made with some caution. In addition to the abovementioned factors (different legal louse limits, different oceans, different sampling gear), sampling place (open or sheltered ocean, fjord, loch, distance from the closest salmon farm or shoreline) and sampling time (season, tides) might influence the observed densities.

Conclusion

The main goal of this thesis was to investigate the development of salmon lice in commercial salmon farming localities and the dispersal potential of their planktonic stages. This was explored through field investigations and the analysis of salmon and salmon lice production data.

Salmon lice numbers were higher during the second year of the production cycle in the study area. For the production cycle starting in 2015, there was an increase in adult female salmon lice in the first year of the production cycle. For a management area, the number of salmon lice can remain high for the area as a whole, even when all localities keep salmon lice below the legal limits of 0.5 adult female lice per salmon.

Localities located downstream of the other localities, or in a connected management area, are likely experiencing a higher external infection pressure when there is salmon production in the area. In order to monitor and control the salmon lice situation, areas with high connectivity among localities should have a system to share lice counts in close to real time, in order to keep the infection pressure low for the area and prevent quick re-infestation of salmon lice.

There was a shift from reliance on medical treatments against salmon lice towards mechanical treatments in the study area. Cleaner fish were deployed earlier during the latest production cycle studied, and localities stocked with ≥4% cleaner fish, showed a delay in time until the salmon reached 0.1 adult female lice per salmon, compared to localities stocked with <4% cleaner fish.

When investigating the link between the number of salmon lice on the salmon and the densities of planktonic sea lice found in plankton samples,

several significant correlations were found. Densities of planktonic sea lice, at cages without lice skirts, correlated positively with temperature both years of the production cycle and also with abundance of adult female lice during the second year. Samples taken from the inside of cages with lice skirts showed these same correlations with the exception of planktonic sea lice not being correlated with temperature the second year of the production cycle. No salmon lice or *C. elongatus* were found in samples taken during the fallowing period. Synchronised fallowing can work as a last resort to curb a salmon lice population growing out of control, at least for areas sufficiently isolated from other production areas.

The investigation into biofouling as a microhabitat for planktonic sea lice showed no evidence for a resuspension of sea lice from biofouling during *in situ* net cleaning with high pressure washers. Only one planktonic sea louse was found in the investigated biofouling. These results suggest that planktonic sea lice are not utilising biofouling as a microhabitat. No difference in the density or prevalence of planktonic sea lice inside or outside of salmon cages without lice skirts was found, regardless of the biofouling coverage. Biofouling on the net was found to not hinder the dispersal of planktonic stages of sea lice out of the cage. A higher prevalence of planktonic sea lice in inside-samples was only found in one of two localities utilising lice skirts.

Future perspectives

Even with half a century of study on salmon lice biology and ecology, there still remain unanswered questions about this parasite and how to control its infestation in salmon farms. This thesis and papers included herein has both answered and spawned new questions for further investigation under the following topics.

Synchronised fallowing and synchronised production cycles

- The benefits and drawback of synchronised fallowing and synchronised production cycles should be outlined, in order to better understand under what circumstances synchronised fallowing could be beneficial.
- Establishment of an optimal size of the management zone for salmon lice control, under different environments; coastal areas, fjords and lochs should be further evaluated.
- Future studies could also assess the required length of fallowing, in order to reduce an area's external infection pressure from both salmon lice and *C. elongatus*.

Cleaner fish and *C. elongatus*

- An investigation into the timing of cleaner fish deployment and what effect it has on the settlement of salmon lice, *C. elongatus*, and the cleaner fish's lice eating efficiency, should be undertaken.
- Development of *C. elongatus* on salmon should be investigated in relation to the use of lice skirts and other management practices.
- Abundance of *C. elongatus* on salmon should be studied in relation to the use of lumpfish, as this is a known host of *C. elongatus*.

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Paper I

ORIGINAL ARTICLE

How are the salmon lice (*Lepeophtheirus salmonis* Krøyer, 1837) in Atlantic salmon farming affected by different control efforts: A case study of an intensive production area with coordinated production cycles and changing delousing practices in 2013–2018

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Abstract

The aims of the present study were to describe the salmon lice (*Lepeophtheirus salmonis* Krøyer, 1837) situation in an intensive salmon production area in mid-Norway and to consider implications of changing practices of how salmon lice infestation can be controlled. The results in this study suggest that there are steps that can be carried out to keep salmon lice under control even during years when the temperature facilitates a quick salmon lice development. The present work indicates that the use of cleaner fish can delay the time it takes adult female lice to reach 0.1 per salmon in the beginning of a production cycle. It suggests that the timing of cleaner fish deployment into salmon cages can influence its effectiveness in controlling salmon lice. It also gives caution to letting salmon lice develop unchecked, even at levels far below the current lice limit, because of the difficulties to control salmon lice when the external infection pressure is too high. This study took place during a rapid change in delousing methods, in an area with coordinated salmon production. Despite its exploratory nature, this study offers insights into the salmon lice fluctuations in relation to efforts aimed at controlling it.

KEYWORDS
cleaner fish, delousing, *Lepeophtheirus salmonis*, preventative methods, salmon aquaculture, salmon lice

1 | INTRODUCTION

In 2017, the first-hand value of Norway's salmon production was 61.6 billion NOK (US$7,226 millions; Baklien & Steinset, 2019), but in recent years, there have been an increasing cost of production. One of the main contributors to this increase in cost, and among the greatest challenge for the salmon industry today, is the parasitic salmon lice (*Lepeophtheirus salmonis* Krøyer, 1837; Costello, 2006; Iversen, Hermansen, Nystøyl, & Hess, 2017; Johnson, Treasurer, Bravo, Nagasawa, & Kabata, 2004). Salmon lice is an ectoparasite with eight life stages, comprised of three planktonic stages (nauplii 1&2, copepodite), two sessile stages (chalimus 1&2) and three mobile stages (preadult 1&2, adult; Hamre et al., 2013). In the copepodite stage, the salmon lice need to find and attach to a host, both

to continue its life cycle and to eat. Before the salmon lice attaches to a host, it relies on energy reserves it got from the egg (Tucker, Sommerville, & Wootten, 2000).

How far salmon lice can spread depends on both temperature and local currents. It is well established from a variety of studies that temperature affects duration of life stages and generation time of salmon lice (Boxaspen & Naess, 2000; Johnson & Albright, 1991; Samsing et al., 2016). Generation time is higher at lower temperatures, and temperatures of 3°C lower both hatching success and development to copepodites (Boxaspen & Naess, 2000; Hayward, Andrews, & Nowak, 2011; Samsing et al., 2016). Planktonic stages of salmon lice drift mostly with the currents, but are capable of dial vertical migration and tend to aggregate in upper parts of the water column (Costelloe, Costelloe, Coghlan, O'Donohoe, & O'Connor, 1998; Costelloe, Costelloe, & Roche, 1996; Heuch, Parsons, & Boxaspen, 1995). Currents in the upper part of the water are influenced by wind speed and direction (Lekang & Fjæra, 1997). Although some research has shown that distribution of planktonic salmon lice was affected by wind (á Norði et al., 2015; Asplin et al., 2014), only a few empirical studies have taken wind into account when describing salmon lice numbers.

When limits for acceptable salmon lice per fish are reached, efforts must be made to reduce lice levels to the legal limits of 0.5 adult female lice. During 6 weeks in the spring, this limit is further lowered to 0.2 adult female lice per salmon (Forskrift om lakselusbekjempelse, 2012). Reduced sensitivity to traditionally delousing methods has forced a change in how salmon is deloused (Overton et al., 2018). This change took place from 2013 to 2017, and several new methods for delousing were implemented during this period (see Table 1).

Lice skirts are perhaps the most common of several technological adaptions aimed at limiting contact between salmon and infestive copepodites in the upper water column, and several studies show reduction of salmon lice on salmon when the method is used (Grøntvedt & Kristoffersen, 2015; Stien et al., 2016; Stien, Lind, Oppedal, Wright, & Seternes, 2018). Rearing cleaner fish together with salmon is also reported to reduce the salmon lice numbers on salmon (Imsland et al., 2014). Two groups of cleaner fish are used in Norway: wrasse (*Labridae* spp) and lumpfish (*Cyclopterus lumpus* Linnaeus, 1758). Fallowing has been suggested to limit settlement of salmon lice in earlier month of a production cycle. This concept has recently been challenged by models demonstrating that a substantial influx of salmon lice larvae from surrounding areas reduced the effect of coordinated fallowing in all areas of the study and leads to a higher parasite density in the later months of the production cycle (Guarracino, Qviller, & Lillehaug, 2018). A growing body of literature recognizes that parasite density in an area is an important factor in the host–parasite relationship, also when it comes to salmon and salmon lice (Frazer, Morton, & Krkosek, 2012; Heuch et al., 2009; Jansen et al., 2012; Kristoffersen et al., 2014). This relation was implemented in the governing of salmon production in Norway in 2017 with implementation of a new management system often referred to as "the traffic light system" (Vollset et al., 2018).

While there have been multiple analyses of salmon lice records (Heuch, Revie, & Gettinby, 2003; Kristoffersen et al., 2014; Lees, Gettinby, & Revie, 2008; Overton et al., 2018), a systematic understanding of how the salmon lice situation is affected by our efforts to control it is still needed to get an in-depth understanding of larger trends. This study systematically reviews data for salmon lice, delousing efforts and number of salmon in a large area in Norway, which practices coordinated production cycles of salmon. This study

TABLE 1 Treatment categories that have been used for delousing salmon (*Salmo salar*) for salmon lice (*Lepeophtheirus salmonis*) in Norway. Time of introduction is given for the category as a whole, and not for individual substances

Medicinal lice treatments: Parenthesis show English name and commercial name (*Italic*) of delousing product	Mechanical lice treatments
<u>Bath treatment</u>: available from 1974 Medicinal bath treatments were the first delousing treatments used in Norway, where the treatment usually consists of reducing the net volume and then covering the salmon cage with a tarpaulin cover before adding the medicaments. Medicaments used for bath treatments can be divided into organophosphates (metrifonate: *Neguvon*; dichlorvos: *Nuvan*; azamethiphos: *Salmosan*), antiseptic (hydrogen peroxide: *Paramove*), pyrethroids (deltamethrin: *Alfamax*; cypermethrin: *Exicis*, *Betamax*) and pyrethrum (*Py-Sal 25*) (Poppe, 1999).	<u>Lice flusher</u>: method developed in 2010. Salmon are in these methods pumped into specialized boats or constructions, where they are subjected to water injectors creating turbulence, and dislodging the salmon lice. Salmon lice are then collected and destroyed by the boat/ construction. There are three companies providing some variant of this method (FLS delousing system, SkaMik and Hydrolicer; Holan et al., 2017).
<u>Oral treatment</u>: available from 1996 Medicinal oral treatments are administered to the salmon through specialized feed. Oral treatments can be divided in two broad categories: chitin synthase inhibitors (diflubenzuron: *Lepsidon*; teflubenzuron: *Ektobann*) and avermectins (Emamectin benzoate: *SLICE*) (Burridge, Weis, Cabello, Pizarro, & Bostick, 2010; Poppe, 1999)	<u>Freshwater treatments</u>: 2011–2013 Freshwater treatments are a bath treatment where they rely on the osmotic shock for salmon lice, and it can be administered inside cages by adding a tarpaulin skirt and creating a freshwater layer, or by pumping salmon into well boats with freshwater (Holan et al., 2017; Reynolds, 2013; Wright, Oppedal, & Dempster, 2016). Freshwater treatments were in use in Australia in mid-1980s, mainly used to treat amoebic gill disease, but the application for the control of salmon lice on a commercial level is new (Powell, Reynolds, & Kristensen, 2015). <u>Thermic treatment</u>: method developed 2014. In thermic treatment, salmon are pumped into specialized boats/ constructions that make them go through a warm water bath (28–34°C), for 20–30 s. The principle is that the smaller salmon lice will be stunned faster than the salmon, and subsequently fall off and are collected for destruction by the boat/ structure (Holan et al., 2017)

covers a time of rapid change in practices of delousing (2013–2018). It aims at providing an overview of salmon lice development during three consecutive production cycles and to consider implications of both changes in delousing methods and increased use of preventative practices, while bearing in mind the environmental effects of temperature, and local wind and current pattern.

2 | MATERIALS AND METHODS

2.1 | Study area

Distribution and infestations of salmon lice on salmon farms were studied in an area in mid-Norway that has a high density of salmon farms. The area is north of Frøya (Figure 1), which is within Norway's production zone 6 (Kristoffersen et al., 2018). This area is characterized by a multitude of smaller islands, reefs and islets. The main current runs from south–west (SW) to north–east (NE) through the archipelago, but the area is also affected by tidal currents through Sulfjord, giving a secondary current running from east (E) to west (W) at ebb tides (B. Johansen, personal communications, 2019 May 6). The study area consisted of 18 farming localities that were active at least once during 2013–2018. Coordination of production cycles

and fallowing periods were established as a strategy in 2013, and since then 12–16 of the localities have been in use during the same production cycle.

Wind data were obtained from the Norwegian Metrological institute (MET Norway). The wind data used in this paper were weather observations from the closest weather station on Sula (63°84′67″N 008°46′67″E, 5 MASL), where measurements of wind speed, direction and air temperature were measured every hour (MET Norway, 2019). After checking for diurnal changes in the wind patterns each month, data were aggregated to daily averages. The wind direction was vectorized as part of averaging, to retain correct direction, and the function timeAverage from R package openair (v2.6-1) was used for this (Grange, 2014). Density of the prevailing wind directions through the year was then calculated using a two-dimensional kernel density estimation from the MASS package (v7.3-51.1), using a bandwidth of 45 for wind direction and 8 for week of the year.

2.2 | Data on salmon production and salmon lice infestations

Information on the number of salmon, and number and type of treatment used against salmon lice for each salmon cage, each week from
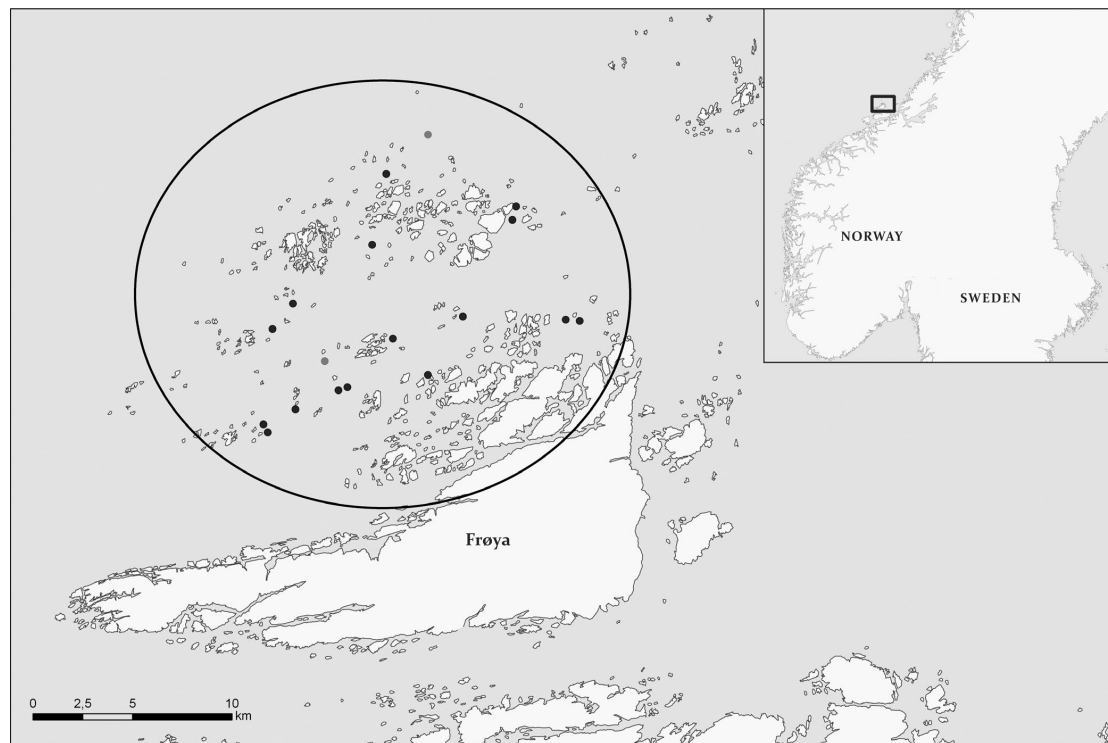
FIGURE 1 Map over study area (inside black circle). The area is located north of the island Frøya in midNorway, around 63.8 N, 8.6 E. Dark circles illustrate salmon localities that had salmon during the summer 2017, and light circles illustrate salmon localities that were in use at least once during 2013–2018. Map created by Tale Skrove. © Kartverket © Europa wms

2013 to 2018, was gathered from all companies producing salmon in the study area. Number of lice per salmon, number cleaner fish deployed, and seawater temperature at 3 m depth from all locations each week were gathered from the Norwegian Food Safety Authorities through BarentsWatch's fish health sites (BarentsWatch, 2019).

Seawater temperature measurements from all localities in the study area and the adjacent area around the island Frøya were used to create a mean seawater temperature each week. Other localities were included to get a year-round measurement of mean seawater temperature, as seawater temperature was only available during the production cycles for the study area. All data were combined into one dataset.

When salmon lice or salmon numbers were not available each week, the latest number of salmon in that cage, or the latest number of salmon lice, was used until the next measurement. For one locality, number of salmon was not available for each week in the last production cycle (2017–2018), and it was then assumed a steady death rate of salmon each week from deployment until slaughter of the salmon. Number of lice per locality was calculated by multiplying the number of salmon with the number of salmon lice in the different lice stage groups, which was recorded in that locality. These numbers were then summed over all localities to give a total for the whole area.

For the number of cages treated each week, the following filters were used: in the case of treatments with a duration of more than one day, as with oral treatment, the starting date of the treatment decided which week the treatment was assigned to. Treatments were divided into the following categories: (a) medicinal bath treatment (including all chemotherapeutants and hydrogen peroxide), (b) oral treatment, (c) freshwater treatment, (d) mechanical treatment by hosing, and (e) mechanical treatment by heat.

Repeated treatments of the same method on the same cage within 5 days were counted as one treatment. There were 112 instances where a combination of treatment products in the same treatment was used. If the methods were in the same category, that is bath treatment and bath treatment, it was counted as one. In the cases where a combination of methods was used (18 cases), that is both bath treatments and oral treatments, the treatments were counted as two treatments. All 112 cases were from 2014 to 2016, and the combination of methods was 9 in both 2015 and 2016. In the end, the dataset was comprised of 311 weeks of observations, where 40 weeks were during following.

Due to lacking numbers on cleaner fish mortality, the survival of cleaner fish throughout the production cycle is unsure. Therefore in this paper, the number of cleaner fish introduced to the salmon cages was used. Two types of cleaner fish were used: Lumpfish (*C. lumpus*) and Wrasses (Ballan wrasse (*Labrus bergylta* Ascanius, 1767), Corcwing wrasse (*Symphodus melops* Linnaeus, 1758), Goldsinny wrasse (*Ctenolabrus rupestris* Linnaeus, 1758) and other wrasse species).

2.3 | Analytical methods

Because of nonlinearity, tests for correlation were done with Spearman rank-order correlation. Tests for differences in groups used Kruskal–Wallis tests, with a follow-up test using Dunn's test. Summary statistics on lice number in text and in tables are given as medium ± medium absolute deviation (MAD) because of the skewed nature of the data. Survival analysis was used to quantify the effects of different variables on the time to a certain lice threshold was reached in each locality during the first year in the sea for each production cycle. Start point for the analysis was set as the first week salmon were deployed for each locality, and time to event was measured in weeks after this. Three survival analyses were fitted, and events were chosen to be first time lice on salmon reached the threshold in each locality. Survival analysis 1 used 0.1 adult female lice per salmon, survival analysis 2 used 0.3 sessile lice per salmon, and survival analysis 3 used 0.3 mobile lice per salmon. Because of the time dependency in the data, left truncation and right censoring
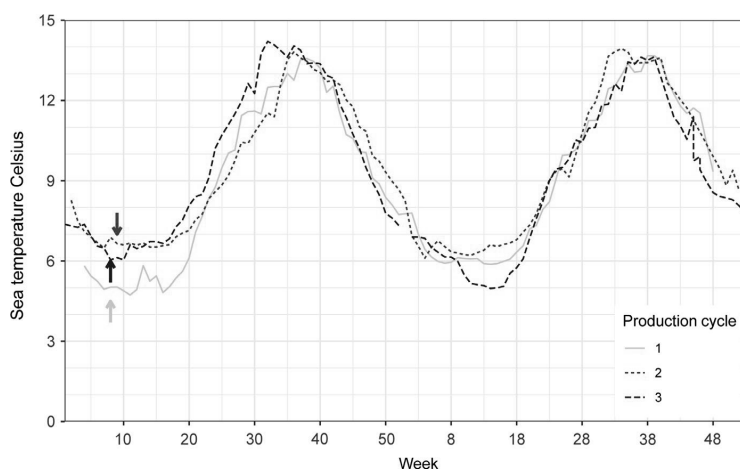
FIGURE 2 Average sea temperature (at 3 m depth) each week for Frøya during the period 2013–2018. The line colour shows different production cycles, Pc1: 2013–2014 (light blue, solid), Pc2: 2015–2016 (dark red, dash) and Pc3: 2017–2018 (dark blue, long dash). The same cohort of salmon are present in the two consecutive years. X-axis shows week number during these 2 years. Y-axis shows mean sea temperature in °C. Arrows indicate where the first salmon arrived for the area

were used each week when the threshold had not been reached. An explanation of survival analysis can be found here (In & Lee, 2018), and an introduction to techniques for censored and truncated data can be found here (Klein & Moschberger, 2003). A univariate survival analysis for different lice thresholds and those factors thought to impact lice levels was performed according to the Kaplan–Meier procedure. Tests for differences in survival curves for different categories of variables were performed with Mantel–Cox statistics. Variables that had a significant effect on survival at an alpha level of 10 in the univariate analysis were further analysed in the multivariate Cox proportional hazard regression model, to investigate which variables had independent effect in the survival curves. The variables were investigated in log minus log plots and by Schoenfeld residual plots in order to test the assumptions about proportional hazard and linearity, both during the univariate and multivariate analyses. Several continuous variables were considered as covariates in the survival analysis, but none held the linearity assumptions when tested as continuous. Suitable threshold values were then chosen, and the variables were included as categorical, if they held the proportional hazard assumption. The final models were chosen based on AIC score and significance of the variables. Only variables that held the assumptions are reported in this paper.

Data were compiled, cleaned and managed using R version 3.5.2 (R Core Team, 2018) in combination with Microsoft Excel 2016. In addition to base R, packages were used in combination with R, most notably the package ggplot2 (v. 3.1.0), which were used to construct all figures except the map in Figure 1 (Wickham, 2016), and the package survival (2.44) was used to run the survival analysis (Therneau, 2015;

Therneau & Grambsch, 2000). For a list of all R packages used, see Appendix S1.

3 | RESULTS

3.1 | Sea temperature

Sea temperature followed the same patterns all years. Differences between production cycles were usually less than 1°C (Figure 2). The largest range in temperature between production cycles is seen during two cold periods in the springs of 2013 and 2018. Pairwise comparisons showed that 2017 was significantly warmer than 2013 during the production cycles, but not significantly different from 2015. Analysing only the period winter–spring (up to week 20) showed that it was significantly colder in 2013 compared to 2017 and 2018 ($\chi^2(2) = 118.04$, $p < .001$). Analysing the period spring–summer (week 8–35) 2017 was significantly warmer compared to both 2013 and 2015 ($\chi^2(2) = 9.12$, $p < .05$).

3.2 | Wind

The wind in the study area usually came from two directions, SW-W and either SE or E (Figure 3a). Wind rarely came directly from south. Data on wind direction were missing for week 2–9 in 2018. The highest wind speeds (m/s) were seen during the winter and were associated with wind directions from W, SE and NE (Figure 3b). The summer period had the lowest wind speeds, which were associated with winds from NE and E.
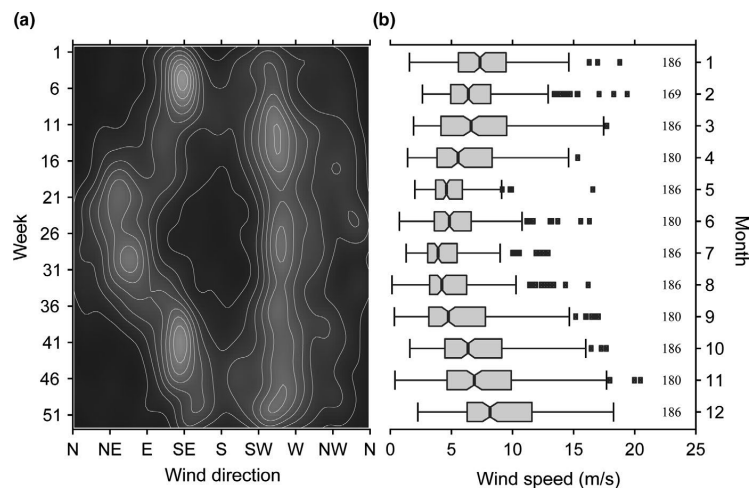
FIGURE 3 Wind direction (where wind is blowing from) and wind speed (m/s) in the study period (2013–2018). (a) Wind direction each week plotted as a density plot, with lighter colours indicating that wind coming from that direction was more common that period. White lines are additional guides for areas with similar density (0.001% per line, range 0.0001–0.001.1%). (b) Boxplot showing monthly wind speed. A boxplot consists of a box reaching from the 25th to the 75th percentile, with a line at the 50th percentile (median). The area inside the box is called the interquartile range (IQR). The notch approximates the 95% confidence interval (CI) for the median and is calculated as 1.58*IQR*square root of the number of values. Whiskers extending out from the top and bottom of the box stretch to the highest/lowest value in the dataset which is still within 1.5 times the IQR. Values outside this are shown as black points (Krzywinski & Altman, 2014)

(a)

Production cycle 1
15.3 milliones

Production cycle 2
18.2 milliones

Production cycle 3
17.6 milliones

Fallowing: 5 weeks

Fallowing: 12 weeks

Fallowing: 16 weeks

Fallowing: 6 weeks ++

Salmon (in millions)

2013   2015   2017   1.

01 18 35   01 18 36 53 17 35 52   18 35 01 18 35 01

| Treated salmon | Adult female lice | 1. Cage treatment |
| Salmon | Mobile lice | Sessile lice | 2. Cleaner fish deployment |

(b)

Salmon & Salmon lice (both in millions)

† 6 points of scale,
(22 - 55 millions)

2015   2017   1.
2.

01 18 35 01 18 36 53 17 35 52 18 35 01 18 35 01

Time, year and week

FIGURE 4 Number of salmon (*Salmo salar*) (a) and number of salmon lice (*Lepeophtheirus salmonis*) (b) for the study area during three production cycles 2013–2014, 2015–2016 and 2017–2018 (time shown on *x*-axis, as year, and week). In plot A, *y*-axis shows number of salmon (black line) and salmon treated for salmon lice (grey area) both in millions. The treatment band above the *x*-axis (numbered 1) shows number of cages treated for salmon lice, where darker colours mean a higher number of cages were treated, and black equals 60 treated cages. The period between production cycles is marked with grey rectangles with duration in weeks. In plot B, *y*-axis shows number of salmon and salmon lice in the area (both in millions), and salmon are shown by the grey line, sessile salmon lice (dotted line), mobile salmon lice (dark grey line) and adult female salmon lice (dark blue area). The cleaner fish band above the *x*-axis (numbered 2.) shows distribution of cleaner fish deployment, with darker colours indicating that more cleaner fish were deployed that week. Salmon numbers and treatment band 1. are the same for both plot A and B. †The 6 points above the scale are here given in millions for each year and week; Sessile lice, 22, 33, 29 and 40 million in year-week 2015–32, 2015–40, 2016–34, 2016–35, respectively. Mobile lice: 22 and 55 million in year-week 2015–40 and 2016–35

3.3 | Production of salmon throughout the period

At the start of the production cycle, there was a rapid deployment of salmon in the area until it reaches the maximum number of salmon, after which it steadily sinks due to salmon mortality, and eventually plummets when salmon are taken out for slaughter (Figure 4a). Maximum number of salmon, number of cages and stocking density are shown in Table 2.

3.4 | Salmon lice through the period

Salmon lice numbers showed considerable fluctuations through the production cycles. The number of sessile and mobile lice increased first, and this increase was steeper and came earlier for Pc2 and Pc3 compared to Pc1 (see later section on Survival analysis). Adult female lice were below 1 million until the winter in Pc1 2nd year and until the beginning of summer in Pc3 2nd year. For Pc2, number of adult female lice reached 5 million already the first summer and stayed above 1.5 million until the salmon were slaughtered at the end of the production cycle. Total number of all lice types showed a significantly increasing correlation with seawater temperature for the first year in the sea (r_s = .33, .54 and .36, p < .001, for sessile, mobile and adult female lice numbers, respectively). Median and MAD of salmon lice for each Pc are found in Table 2.

3.5 | Treatments against salmon lice through the period

Total numbers of cages treated against salmon lice for the whole period were 914 (898, Figure 5). Number of cages treated in each Pc was 262, 550 (534) and 102 in Pc1, Pc2 and Pc3, respectively. Numbers in parenthesis indicate number of cages treated when accounted for multiple treatments of different method at the same time. Only medicinal delousing was in use in Pc1 2nd year, but the percentage of treatments using medicinal delousing fell to 36% in Pc3 (Table 3). Mechanical treatments accounted for 51% of the treatments the production cycle they were introduced (Pc2) and increased to 64% of the treatments in Pc3.

3.6 | Use of lice skirts and cleaner fish through the period

Lice skirts were introduced to the area in Pc2 with 12 cages using lice skirts during the whole production cycle. In Pc3, this number increased to 66 cages, and 61 retained lice skirt on during the whole production cycle. This equals a fivefold increase in coverage from 10% to 50% between the two production cycles. In Pc3, median lice in the localities with lice skirts on during the entire production cycle were higher compared to localities without lice skirts for adult female lice (with lice skirt: 0.03 ± 0.05, without lice skirt: 0.01 ± 0.01, χ^2(1) = 25.1,

TABLE 2 Shows production numbers for the study period, with maximum number of salmon, and salmon cages each production cycle (Pc), beginning stocking density of salmon per cage

Production cycle (first year–second year)	Pc1 (2013–2014)	Pc2 (2015–2016)	Pc3 (2017–2018)
Maximum number of salmon (millions)	15.3	18.2	17.6
Maximum number of salmon cages first year–second year	88–98	117–120	121–121
Number of salmon per cage, at beginning of production cycle (thousand)	173	156	145
Adult female lice per salmon, median ± MAD	0.00 (0.01)*	0.12 (0.18)*	0.03 (0.04)*
Mobile lice per salmon, median ± MAD	0.10 (0.15)*	0.44 (0.52)*	0.14 (0.16)*
Sessile lice per salmon, median ± MAD	0.03 (0.04)*	0.11 (0.16)*	0.4 (0.06)*

Note: Median ± median absolute deviation (MAD) are shown for each Pc, and marked with if * significantly difference from the other Pc, when compared in Kruskal–Wallis tests.
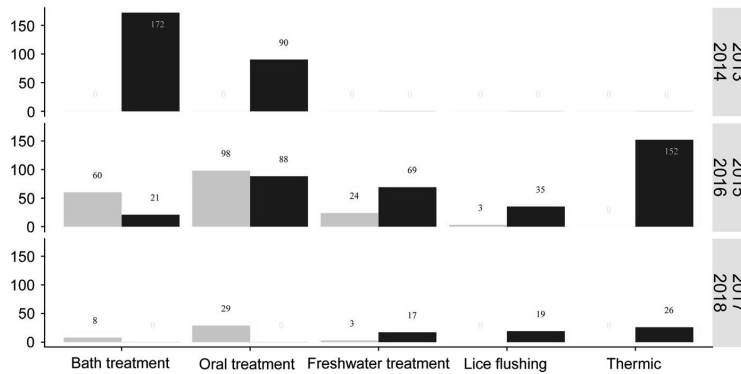
FIGURE 5 Delousing events that occurred in the study area. Number of cages treated with each delousing method is shown. The different production cycles are shown in each row on the *y*-axis (light blue represents the first production year, and the dark blue represents the second year of the production cycle). Method of delousing is shown on the *x*-axis

TABLE 3 Relative (%) use of each salmon lice (*Lepeophtheirus salmonis*) treatment during three production cycles (2013–2018)

Year (production cycle)	Medicinal treatment (%)			Mechanical treatment (%)			
	Bath	Oral	Total medicinal	Freshwater	Thermic	Lice flusher	Total mechanical
2013 (1)	0	0	0	0	0	0	0
2014 (1)	66	34	100	0	0	0	0
Total (1)	66	34	100	0	0	0	0
2015 (2)	32	53	85	13	0	2	15
2016 (2)	6	24	30	19	42	10	70
Total (2)	15	34	49	17	28	7	51
2017 (3)	20	73	93	8	0	0	8
2018 (3)	0	0	0	27	42	31	100
Total (3)	8	28	36	20	25	19	64

Note: Medicinal treatment includes bath treatment and oral treatment. Mechanical treatment includes freshwater, thermic and lice flushing treatments. Summed values of area given for both each production cycle and medicinal and mechanical treatments (grey shaded area).

$p < .001$) and mobile lice (with lice skirt: 0.15 ± 0.17, without lice skirt: 0.09 ± 0.10, $\chi^2(1) = 5.49$, $p < .05$), but not for sessile lice (with lice skirt: 0.02 ± 0.03, without lice skirt: 0.03 ± 0.04, $\chi^2(1) = 3.80$, $p = .05$).

Wrasse was the most common cleaner fish used in Pc1 (94%), but with the inclusion of lumpfish the next production cycle it fell to 43% before the number of wrasse and lumpfish was equal (49% wrasse, 51% lumpfish; Figure 6). Most cleaner fish were deployed during the first year of the production cycle (86%–89%), and timing of the first cleaner fish deployments came earlier in Pc3 (6.0 ± 5.9 weeks) compared to Pc2 (17.5 ± 7.4 weeks) and Pc1 (16 ± 4.5) ($\chi^2(1) = 2.74$, $p < .01$), numbers in parenthesis show median ± MAD. The distribution band shows that there was a regular refill of cleaner fish throughout Pc3 (Figures 6 and 4b).

3.7 | Survival analysis

Survival analysis 1 shows that the cleaner fish level (4%), production cycle and the observation of adult female lice in the area the prior week were significantly related to the time it took before a locality reached 0.1 adult female lice per salmon (Table 4). The lowest risk of reaching the threshold from one week to another was found for localities in Pc1 and Pc3 which had more than 4% cleaner fish, when

there was reported 0 adult female lice the week before ($\chi^2(4) = 56.8$: $p < .001$, concordance 0.84, AIC 305).

Survival analysis 2 shows that the production cycle, cleaner fish level (2%) and the observation of sessile lice on the same locality the week prior were significantly related to the time it took a locality to reach 0.3 sessile lice (Table 4) ($\chi^2(4) = 78.8$: $p < .001$, concordance 0.85, AIC: 339). The lowest risk of reaching the threshold of 0.3 sessile lice per salmon from 1 week to another was found for localities in production cycle 1 that had more than 2% cleaner fish, when there was reported 0.1 or less sessile lice at that locality the prior week.

Survival analysis 3 shows that the production cycle and cleaner fish level (5%) were significantly related to the time before a locality reached 0.3 mobile lice (Table 4) ($\chi^2(3) = 82.5$: $p < .001$, concordance 0.81, AIC 355). The lowest risk of reaching 0.3 mobile lice was found for localities in Pc1, who had a stoking density below 5% cleaner fish.

4 | DISCUSSION

There was a significantly increasing relationship between the lice numbers of all lice stages and the sea temperature, which

FIGURE 6 Number of cleaner fish deployed in the study area during three production cycles 2013–2014, 2015–2016 and 2017–2018 (time in years shown on x-axis). Number of Wrasse (Labridae spp.) (light blue) and Lumpfish (*Cyclopterus lumpus*) (dark blue) in thousand (y-axis) is shown for each year (x-axis). Distribution of cleaner fish deployment through the year is shown underneath the bars with start of production cycle indicated as black vertical lines
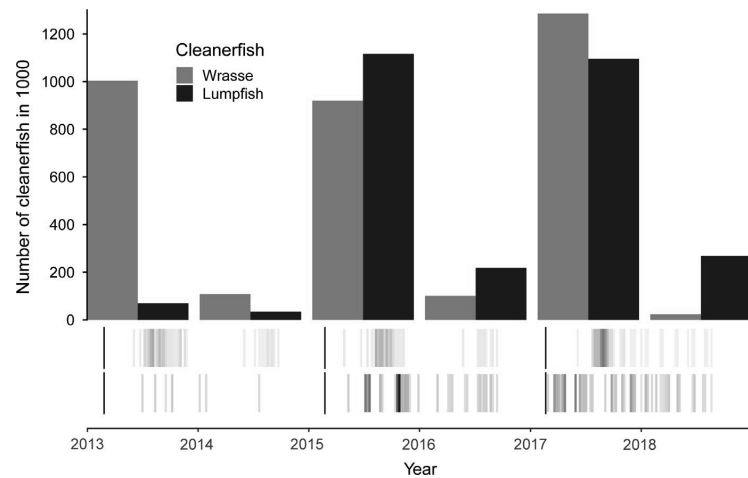
is in accordance with the literature (Boxaspen & Naess, 2000; Johnson & Albright, 1991; Rees et al., 2015; Samsing et al., 2016). The time from deployment until 0.3 sessile lice were reached for the first locality was 20, 6 and 14 weeks for Pc1, Pc2 and Pc3, respectively. The time difference could be the result of lower temperatures in the beginning of Pc1 and Pc3 as shown in Figure 2. Although 2017 was significantly warmer compared to 2015 for the first half year of the Pc (week 8–35, H(2) = 9.12, p < .05), when limiting the analysis to weeks 8–12, 2017 was significantly colder compared to 2015 (H(2) = 7.53, p < .05), as can be seen as a dip in temperature in Figure 2. Sessile salmon lice appear to have limited infection capabilities when temperatures are close to or below 6°C. A lower success of settlement at lower temperatures fits with earlier studies, where Samsing et al. (2016) found an infestation success of less than 5% for copepodites at 5°C, which rose to 50% at 10°C.

The currents in the area fluctuated with the tides and run towards E-NE with flow tide, and towards W or SW with ebb tides (personal observation from field, locality reports (NYTEK-forskriften, 2019) and coastal forecast from Yr (https://www.yr.no/place/Ocean/63.78400_8.53514/). Since this area has semidiurnal tides, this means that the current could change direction four times a day. Wind direction has in earlier studies been found to affect the distribution of planktonic salmon lice (á Norði et al., 2015). From salmon farm locality reports in the area, wind was deemed to have most effect on the surface current when they coincided with either the main or secondary current direction and came from E or W. Figure 3a shows that winds from SW-W were usual throughout the year and that winds from E were more common during the summer. Most of the year the winds therefore contributed to the main current, while during the summer when temperatures already make the salmon lice into a bigger problem, the winds contributed to the secondary current in the area. It seems that there may be an association between the timing of wind direction change to wind blowing from NE-SE and the timing of the increase in sessile lice on the salmon (individual

figures per years not shown) but studying this falls without the scope of this paper.

4.1 | Salmon lice in the area

Salmon lice of all stages were significantly higher in Pc2 (Table 2). All lice types were significantly higher in the second year of the sea (adult female lice: $\chi^2(1) = 785$, p < .001, mobile lice: $\chi^2(1) = 259$, p < .001, sessile lice: $\chi^2(1) = 29$, p < .001). These results are in accordance with earlier studies stating that salmon lice are usually a more prominent problem in the second year of the production cycle. This has been attributed to that salmon have spent more time exposed to the salmon lice recruitment from the environment (Jackson, Hassett, Deady, & Leahy, 2000; Revie, Gettinby, Treasurer, Rae, & Clark, 2002). The results from the survival analysis of both sessile and adult female lice also showed the first year of Pc2 as having significantly shorter time before the threshold was reached. Survival analysis on 0.3 mobile salmon lice threshold showed that there was no significant difference between the hazard ratios for Pc2 and Pc3, which can also be seen from the slopes of mobile lice in Figure 4b. This suggests a quicker maturation of the sessile salmon lice in Pc3, which is in accordance with the higher temperatures seen during this spring. The temperature during the first week in the sea was included as a categorical variable in the analysis because it had a significant effect on the time to 0.3 sessile and 0.3 mobile lice in the univariate analysis. However, this effect was no longer significant when adjusted for production cycle. This could be because the variable production cycle would also include the variation in temperature seen between the years.

The first lice settling has to come from an external source, and Kristoffersen et al. (2014) showed that the initial settlement period was strongly correlated with their estimated external infection pressure, representing copepodites produced from salmon farms in the vicinity. Guarracino et al. (2018) argue that the increase in salmon lice towards the end of the production cycle, and the existence of an

Covariables	Unadjusted hazard ratio (univariate; 95% CI)	Adjusted hazard ratio (multivariate; 95% CI)
Survival analysis 1. Threshold: 0.1 adult female lice		
Production cycle		
3	1	1
2	10.6 (4.50–24.8)*	10.41 (4.32–25.10) *
1	0.394 (0.123–1.26)	0.67 (0.20–2.25)
Cleaner fish (4%)		
<4%	1	1
≥4%	0.405 (0.195–0.843)*	0.38 (0.18–0.84) *
Adult salmon lice in the area the week before		
0	1	1
>0	5.4 (1.29–22.8)*	3.96 (1.31–11.99)*
Survival analysis 2. Threshold: 0.3 sessile lice		
Production cycle		
3	1	1
2	20.1 (8.38–48.3)*	9.32 (3.69–23.5)*
1	0.365 (0.139–0.961)*	0.324 (0.113–0.927)*
Cleaner fish (2%)		
<2%	1	1
≥2%	0.405 (0.195–0.843)*	0.252 (0.107–0.590)*
Sessile salmon lice on the same locality the prior week		
≤0.1	1	1
>0.1	5.58 (2.83–11.0)*	3.04 (1.46–6.32)*
Average sea temperature first week		
<6.5	1	1
≥6.5	3.04 (1.23–7.55)*	1.92 (0.758–4.87)
Survival analysis 3. Threshold: 0.3 mobile lice		
Production cycle		
3	1	1
2	0.72 (0.36–1.43)	0.765 (0.382–1.530)
1	0.026 (0.009–0.073)*	0.026 (0.009–0.073)*
Cleaner fish (5%)		
<5%	1	1
≥5%	2.21 (1.12–4.43)*	2.205 (1.109–4.388)*
Average sea temperature first week		
<6.5	1	1
≥6.5	3.88 (1.72–8.73)*	0.754 (0.245–2.290)

Note: Effect size is given as hazard ratio, with 95% confidence intervals, and significant ($p < .05$) hazard ratios are marked with *.

external infection pressure at the beginning of a production cycle, puts the effectiveness of coordinated fallowing against salmon lice up for serious questioning. Both arguments of Guarracinos applies for this area, the lice levels during the first summer in Pc2 brings up the question of what would have happened if the area were not practicing a coordinated production cycle. Further investigation into the number of sessile lice per salmon each year showed that there was no significant difference in the number of sessile lice between

2015 and 2016 ($\chi^2(1) = 0.59$, $p > .05$). 2015 had significantly more lice than all other years except 2016 (test between years; $\chi^2(5) = 455$, $p < .001$). As the initial settlement of salmon lice matures, copepodites originating in the area can contribute to a higher infection pressure. Sessile lice reached 22 million only 3 weeks after the first peak in adult female lice in Pc2 (Figure 4b). Without a coordination of the production cycle in this area, the increase in salmon lice would likely have happened earlier this year, due to the high potential for

reinfection brought about from the tidal currents. Adult female lice persisted at more than 1.5 million from the first summer and during the rest of Pc2. This would make it possible for high levels of co-pepodites to be produced in the area and quickly reinfect salmon after delousing. A number of 1.5 million adult female lice, for this area with around 15 million fish, equate to 0.1 per salmon, which is well below the legal limit. This emphasizes that density of salmon lice is important and that there is a need for a coordination of de-lousing activity in an area where lice readily can travel from locality to locality.

4.2 | Salmon lice and treatment

In 2014, it was discovered an increasing resistance towards two common bath treatments (azamethiphos and deltamethrin) and an oral treatment (emamectin benzoate) in the study area (Bornø & Lie, 2015). The higher lice levels in Pc1 2nd year and Pc2 could therefore have been explained by lower treatment efficiency, as have been suggested being the case for high salmon lice numbers in a study from Scotland over 10 years earlier (Heuch et al., 2003). Towards the end of Pc2, bath treatments seem to be the last resort, as it was the least used treatment in Pc2 2nd year. The average number of treatments against salmon lice per cage was 2.7, 4.6 and 0.8 for Pc1, Pc2 and Pc3, respectively. It seems possible that these results, in ad-dition to reflect the higher lice numbers in Pc2, could have been be-cause of the lower treatment efficiency expected when salmon lice develop resistance. It could also have been because the newly intro-duced thermal treatment is most efficient at killing the mobile and adult stages of salmon lice, which Overton et al. (2018) suggested to shorten the time until adult salmon developed on the salmon. In addition to the change in delousing methods, there is a trend to-wards earlier delousing. The proportion of treatments done in the first year was raised to 34% and 39% for Pc2 and Pc3, respectively, compared to 0% in Pc1. From the treatment band in Figure 4b, it can be seen that in Pc2 1st year the first delousing came 3 weeks after the first peek in adult female lice. There was a top in adult female lice of similar height in Pc3 1st year, but at that time a treatment period treating 25 cages with oral treatments had already begun, and adult female lice were held below 1 million until the next year.

4.3 | Salmon lice and precautionary actions

The precautionary actions seen in this area were an increase in use of lice skirt, a longer fallowing period and an increase in the use of cleaner fish. The use of lice skirts or not was done on a locality basis, and the localities without lice skirts were located in the same vicinity of the study area. The significant differences seen in lice numbers for these localities should be taken with a grain of salt, as they are only from Pc3, and it might be an artefact of the geographical separation of these localities. The number of cleaner fish used was more than doubled from Pc1 to Pc3. This in-crease came predominantly from the substantial increased use of lumpfish (1 227% increase from Pc1 to Pc3), but also the number

of wrasse increased by 18%. Use of lumpfish allowed cleaner fish to be deployed earlier in the production cycle as lumpfish can tolerate colder temperatures than wrasses (Nytrø et al., 2014). Although there were more cleaner fish deployed in Pc3 compared to Pc2, there were no significant differences in the numbers deployed ($\chi^2(1) = 0.39$, $p > .05$), making it difficult to argue that share number of deployed cleaner fish could explain the differ-ences seen in lice level. However, the first deployments of cleaner fish came significantly earlier. In Pc1 and Pc3, cleaner fish were deployed in the area before or at the time when the salmon lice started to increase, which was not the case in Pc2. Therefore, in addition to being more numerous in Pc3, the cleaner fish might also have been more effective because they had a few weeks to acclimate to the environment before the increase in salmon lice started.

The three survival analyses all showed significant effects of using cleaner fish. Stocking of cleaner fish at 4% or higher reduced the risk of reaching 0.1 adult female lice by 62% when compared with lower numbers or no cleaner fish. Survival analysis 2 also showed that a cleaner fish stocking of 2% or more gave a 71% reduction in the risk of reaching 0.3 sessile lice. In survival analysis 3, stoking cleaner fish at more than 5% showed an increased risk in reaching the thresh-old, by 120%. Cleaner fish therefore seems to have a different ef-fect on the three lice stages. In an earlier study, lumpfish have been shown to prefer the larger adult female lice (Imsland et al., 2018). From survival analysis 1, we saw that cleaner fish of 4% or more had a delaying effect on the time before 0.1 adult female was reached. The higher risk of reaching 0.3 mobile lice associated with cleaner fish might therefore be because of this prolonged time with lower levels of adult female lice. This would give more time for sessile lice to develop to mobile lice, as it would also prolonging the time before a delousing would be necessary.

In conclusion, the aim of the present work was to examine and describe the salmon lice infestation, and to consider implications of the changing practices of how salmon lice is controlled. This was done in an area with intensive production of salmon that use coordinated production cycles. During these years, a rapid change in delousing methods was happening. The results suggest that temperature is an important factor for the development and in-festation of salmon lice on the salmon. However, some steps can be taken in order to keep the number of salmon lice under control even in years when the temperature facilitates a quick salmon lice development. This study offers insights into the salmon lice fluc-tuations in relation to efforts aimed at controlling it, suggesting the importance of the effectiveness of treatment methods used. It also gives caution to letting salmon lice develop unchecked, even at levels far below the lice limit, because of the difficulties to con-trol salmon lice when the infection pressure is too high. This study indicates that the use of cleaner fish can delay the time it takes for adult salmon lice to reach levels of 0.1 per salmon in the beginning of a production cycle, suggesting that at least some preventative actions against salmon lice do work. A natural progression of this work is to investigate how the timing of cleaner fish deployment is

on the effectiveness in controlling salmon lice, and to explore the densities of planktonic salmon lice around salmon farms during a production cycle to characterize the infection pressure of salmon lice. Further research should examine how the implementation of precautionary methods like lice skirts affects the salmon lice situation in larger areas and not only on a salmon farm level.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data used for this study were both production data that are not available for publicity and open datasets that are referred to in the text.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Paper II

This paper is awaiting publication and is not included in NTNU Open

Paper III

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Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statoliths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalation of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway

1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod (*Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum*. Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density

2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):* Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens.*
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment

2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus)* habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2

2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.

2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on *Arabidopsis thaliana*
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (*Salmo salar*)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological contex to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh

2019	Knut Jørgen Egelie	Phd Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
2019	Thomas Ray Haaland	Phd Biology	Adaptive responses to enviromental stochasticity on different evolutionary time-scales
2019	Kwaslema Malle Hariohay	Phd Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Mari Engvig Løseth	Phd Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (*Haliaeetis albicilla*) nestlings
2019	Joseph Mbyati Mukeka	Phd Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	Phd Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
2019	Nathalie Briels	Phd Biology	Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies
2019	Anders L.Kolstad	Phd Biology	Moose browsing effects on boreal production forests – implications for ecosystems and human society
2019	Bart Peeters	Phd Biology	Population dynamics under climate change ad harvesting: Results from the high Arctic Svalbard reindeer
2019	Alex Kojo Datsomor	Phd Biology	The molecular basis of long chain polyunsaturated fatty acid (LC-PUFA) biosynthesis in Atlantic salmon (*Salmo salar L*): In vivo functions, functional redundancy and transcriptional regulation of LC-PUFA biosynthetic enzymes
2020	Ingun Næve	Phd Biology	Development of non-invasive methods using ultrasound technology in monitoring of Atlantic salmon (*Salmo Salar*) production and reproduction
2020	Rachael Morgan	Phd Biology	Physiological plasticity and evolution of thermal performance in zebrafish
2020	Mahsa Jalili	Phd Biology	Effects of different dietary ingredients on the immune responses and antioxidant status in Atlantic salmon (*Salmo salar L.):* possible nutriomics approaches
2020	Haiqing Wang	Phd Biology	Utilization of the polychaete Hediste diversicolor (O.F. Millier, 1776) in recycling waste nutrients from land-based fish farms for valueadding applications'
2020	Louis Hunninck	Phd Biology	Physiological and behavioral adaptations of impala to anthropogenic disturbances in the Serengeti ecosystems
2020	Kate Layton-Matthews	Phd Biology	Demographic consequences of rapid climate change and density dependence in migratory Arctic geese
2020	Amit Kumar Sharma	Phd Biology	Genome editing of marine algae: Technology development and use of the CRISPR/Cas9 system for studies of light harvesting complexes and regulation of phosphate homeostasis
2020	Lars Rød-Eriksen	Phd Biology	Drivers of change in meso-carnivore distributions in a northern ecosystem