Norwegian University of Life Sciences
Faculty of Veterinary Medicine
Department of Production Animal Clinical Sciences

Philosophiae Doctor (PhD)
Thesis 2023:61

What is the value of a dead fish? The biological and economic impact of delousing farmed Atlantic salmon in Norway

Hva er verdien av en død fisk? Den biologiske og økonomiske betydningen av avlusning av oppdrettet atlantisk laks i Norge

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Now small fowls flew screaming over the yet yawning
gulf; a sullen white surf beat against its steep sides;
then all collapsed; and the great shroud of the sea
rolled on as it rolled five thousand years ago.
-Herman Melville, *Moby Dick*, 1851

In the long run we are all dead.
-John Maynard Keynes, *A tract on Monetary Reform*, 1923

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Os, May 2023
Cecilie Sviland Walde

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1 Abbreviations and definitions

AGD	Amoebic gill disease.
AIC	Akaike information criterion.
bFCR	Biological feed conversion ratio.
Biological loss	Loss of biomass due to mortality and decreased growth.
Cluster	Natural or convenient collection of study subjects with one or more characteristics in common.
Cohort	Group of fish stocked at the same time within the same cage within the same site.
Delousing	Immediate treatment to remove lice from salmon.
Delousing regime	When, how many, and what type of delousing methods are applied during a production cycle.
Externality	An indirect cost (or benefit) to an uninvolved third party that arises because of another party's activity.
Fish-group	Group of fish transferred to the same cage at sea at the same time.
Generation	Salmon from the same year-class, stocked at sea in either spring or fall.
ICC	Intra-class correlation, the correlation between two observations within a cluster.
IPM	Integrated pest management.
ISA	Infectious salmon anaemia.
Mortality rate	Number of deaths in a population per unit of animal time during a given time period/incidence rate describing the speed at which animals are at risk of dying.
Open population	A population that animals are leaving and entering throughout the study period.
PA	Production area.
Parr	Life-stage of salmon before smoltification.
PD	Pancreas disease.
Production cycle	Number of production days from stocking a fish-group at sea until it is harvested.

Site	A farm or seawater facility.
Stocking	Transfer of fish from freshwater facility to seawater site.
Smolt	Life-stage of salmon when a suite of physiological and morphological changes indicates the transition, called smoltification, from living in freshwater to seawater.
Smolt type	Either 1 or 0-yearling. The 1-yearlings are stocked in the spring the year after they hatch, and the 0-yearlings are typically stocked in the fall the same year they hatch.
TGC	Thermal growth coefficient.
Year-class	Salmon stocked at sea in the same calendar year; one year-class comprises two generations.

2 List of papers

Paper I

Cecilie Sviland Walde, Britt Bang Jensen, Jostein Mulder Pettersen, Marit Stormoen

'Estimating cage-level mortality distributions following different delousing treatments of Atlantic salmon (*Salmo salar*) in Norway.'

Published: *Journal of Fish Diseases* 44 (2021), 899-912

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Paper II

Cecilie Sviland Walde, Marit Stormoen, Jostein Mulder Pettersen, David Persson, Magnus Vikan Røseg, Britt Bang Jensen

'How delousing affects the short-term growth of Atlantic salmon.'

Published: *Aquaculture* 561 (2022)

https://doi.org/10.1016/j.aquaculture.2022.738720 (open access)

Paper III

Cecilie Sviland Walde, Britt Bang Jensen, Marit Stormoen, Frank Asche, Bård Misund, Jostein Mulder Pettersen

'The economics of preventing, replacing or improving methods for delousing farmed Atlantic salmon in Norway.'

Submitted: *Journal of Preventive Veterinary Medicine* (24.02.2023)

3 Abstract

The impacts of the ectoparasite salmon lice (*Lepeoptheirus salmonis* (Krøyer, 1837)), is a major challenge for sustainable production of farmed Atlantic salmon (*Salmo salar*) in Norway, and has been so for over 40 years. The challenge with salmon lice, especially the control of it, is the expense and that lice affect different aspects of the economy, environment, and society. Lice have become central to the governmental regulation of the growth of the salmon aquaculture industry, and the most important obstacle to the stated political goal of quintupling aquaculture production in Norway by 2050. The main reason for control is the spillover of lice from farmed to wild salmon. For many years, lice were controlled by use of pesticides. However, they eventually developed resistance to most of the pesticides available. This led to a paradigm shift from treating medicinally to non-medicinally around 2015. Non-medicinal treatments mainly involve the use of heated water baths (thermal treatment) or brushing or flushing (mechanical treatment) of the fish to remove the lice.

In 2020, 52 million salmon, 14.8% of the standing stock, died during the on-growing period at sea. It was suspected that a large part of this mortality was caused by non-medicinal treatments. Veterinarians working in the field had, for several years, raised concerns regarding poor fish health and welfare related to especially thermal treatment. Still, at the on-set of this PhD, we did not know how many salmon died because of these treatments, nor how the treatments affected their growth. Securing good health and welfare is part of sustainable animal production and should be a top priority. Yet, when we do not know the extent of mortality and growth loss associated with delousing treatments, it is difficult to assess how much could be spent on measures to reduce mortality and secure good growth. Consequently, it is also difficult to evaluate how highly we should prioritise work related to reducing mortality and securing good growth after treatment. The main aim of this thesis was therefore to assess the biological and economic impact of treatments against salmon lice.

Based on a unique dataset describing daily production at cage level from 2014-2019 from three large Norwegian aquaculture companies, the increased mortality (paper I) and decreased growth (paper II) associated with different delousing methods

were estimated. Importantly, the results showed that non-medicinal treatments on average had a negative impact on fish health and welfare. Mortality was 5.4 (thermal) to 6.3 (mechanical) times higher after non-medicinal treatments compared to medicinal treatments, for the 2017 year-class. In an average cage containing 150 000 fish, a median of 790 or 928 fish were at risk of dying within two weeks after thermal and mechanical treatment, respectively. This risk varied substantially, and in an average cage the maximum number of dead could be as high as 20 130 or 50 915 after a thermal or mechanical treatment. The median mortality rate decreased two weeks after non-medicinal treatments, but not to the level it was before treatment. The results also showed that the treated fish had an appetite drop that lasted on average one week. The appetite drop was significantly larger following non-medicinal compared to medicinal treatments. For fish weighing on average 3 kg, being treated when the seawater temperature was at 10°C, this appetite drop led to an estimated average growth loss of 51.5±7.5 g/fish non-medicinal treated compared to 33.9±10.5 g/fish medicinally treated. A week of starvation prior to the treatment led to an additional growth loss of 155g/fish. Thus, in a cage containing 150 000 fish, the growth loss due to starvation and suboptimal feeding after one non-medicinal treatment was equal to 31 200 kg compared to not being treated at all. This showed that although the pre-treatment starvation period made up the largest part of the growth loss (~75%), it is important to include the potential growth loss after treatment (~25%). Both studies showed a substantial variation within and between treatment methods, especially within thermal treatment, indicating a potential for improvement if risk factors for increased mortality and reduced growth could be identified and mitigated. In paper II, results suggested that the outcome of a treatment might be influenced primarily by factors such as treatment-related handling procedures, environmental conditions, or disease status of the fish-group.

The results further showed a reduction in median mortality after thermal treatment over the study period, indicating a possible improvement of the technique over the years 2015 to 2019. However, non-medicinal treatment is still regarded as one of the main causes of reduced health and welfare of salmon. Both mortality in the on-growing period at sea and the overall number of non-medicinal treatments were at all-time high in 2022.

Mortality and growth reduction constitutes both a challenge for fish health and welfare as well as a biological loss for the farmer. The extent of this biological loss was implemented in a bio-economic model to assess the economic consequence (costs and benefits) for a farmer of choosing different delousing treatment regimes. We did this by using a stochastic partial budgeting approach. The calculations implied that salmon producers could invest a considerable amount in measures for prevention or improvement of thermal treatments before break-even. For example, a farmer could spend on average 5.4 million NOK (535 313 €) per cage per 1-yearling production cycle on measures to prevent four thermal treatments before it was no longer economically beneficial. Depending on the performance of the four thermal treatments, 3.2 to 7.4 million NOK (319 196 -737 934 €) per cage per 1-yearling production cycle could be spent on measures of improvement. The bio-economic model highlights the importance of incorporating the risk of increased mortality and reduced growth associated with different treatments. It also calls attention to the economic incentive and the need to prioritise work on improving methods to ensure good health and welfare for the salmon.

The work from this PhD shows that knowledge of both the effect from treatment measures and their side effects is important when deciding on treatment strategies. Accounting for the biological losses associated with lice treatments is essential when making choices of delousing strategies. The principles of integrated pest management should be emphasised to ensure a sustainable management of salmon lice in the years to come. Consequently, there is a need to continue to find alternative solutions for both managing and regulating salmon lice in Norway. This should be done through interdisciplinary research and by comparing all the different aspects of the impact of salmon lice against each other.

4 Norsk sammendrag

Lakselus (*Lepeoptheirus salmonis* (Krøyer, 1837)) er en betydelig utfordring for en bærekraftig produksjon av oppdrettet atlantisk laks (*Salmo salar*) i Norge, og har vært det i over 40 år. Utfordringen med lakselus, særlig kontroll av lus, er kostbart og påvirker økonomi, miljø og samfunn. I dag utgjør den et sentralt element i regulering for en bærekraftig vekst av norsk oppdrettslaks, og lus er den viktigste hindringen for den politiske målsetningen om å femdoble akvakulturproduksjonen i Norge innen 2050. Lakselus påvirker bestanden av villaks og de strenge reguleringene er i hovedsak for å hindre at lus fra oppdrettslaksen reduserer lokale villakspopulasjoner langs kysten. I mange år ble lakselus kontrollert ved bruk av antiparasittære legemidler. Imidlertid utviklet lusen etter hvert resistens mot de fleste tilgjengelige midlene. Rundt 2015 førte dette til et paradigmeskift fra medikamentell behandling til ikke-medikamentell behandling. Ikke medikamentelle metoder innebærer i hovedsak å bade laksen i oppvarmet vann (termisk behandling) eller børste og eller spyle (mekanisk behandling) laksen for å fjerne lusen.

I 2020 døde 52 millioner laks i løpet av perioden i sjø, noe som utgjorde 14,8% av bestanden. En regnet med at de ikke-medikamentelle behandlingene trolig forklarte en stor del av denne dødeligheten. Veterinærer som jobbet i felt hadde i flere år uttrykt bekymring angående dårlig fiskehelse og velferd knyttet spesielt til termisk behandling. Likevel visste vi ikke hvor høy dødelighet som var knyttet til de ikke-medikamentelle behandlingene, eller hvordan de påvirket veksten til fisken. Å sikre god fiskehelse og velferd er en del av bærekraftig dyreproduksjon og bør være høyt prioritert. Men, når vi ikke kjenner omfanget av dødelighet og tilveksttap er det vanskelig å vurdere hvor høyt man skal prioritere arbeid med å redusere dødelighet og sikre god vekst i forbindelse med avlusingsbehandlinger. Hovedmålet med denne avhandlingen var derfor å vurdere de biologiske og økonomiske konsekvensene av behandlinger mot lakselus.

Det ble samlet inn data fra tre store norske oppdrettsselskaper som beskrev daglig produksjon på merdnivå i perioden 2014 til 2019. Dødelighet (paper I) og tilveksttap (paper II) assosiert med ulike avlusningsmetoder ble estimert basert på disse dataene. De ikke-medikamentelle behandlingene hadde en negativ innvirkning på fiskens helse og velferd. Dødeligheten var 5,4 (termisk) til 6,3 (mekanisk) ganger høyere etter ikke-medikamentelle behandlinger sammenlignet med medikamentelle behandlinger for 2017 årsklassen. I en gjennomsnittlig merd med 150 000 fisk var det mediant 790 og 928 fisk som var i risiko for å dø to uker etter henholdsvis termisk eller mekanisk behandling. Dette varierte betydelig, og antallet døde i en gjennomsnittlig merd kunne være så høyt som 20 130 (termisk) eller 50 915 (mekanisk). Median dødelighet var nedadgående i en to ukers periode etter ikke-medikamentelle behandlinger, men sank ikke til det nivået den var før behandling. Resultatene viste også at behandlet fisk hadde en nedsatt appetitt som varte i gjennomsnitt én uke. Appetittreduksjonen var betydelig større for ikke-medikamentelle behandlinger enn for medikamentelle behandlinger. For fisk med en gjennomsnittsvekt på 3 kg som ble behandlet når sjøtemperaturen var 10 °C, resulterte dette i et estimert tilveksttap på 51,5 ± 7,5 g/fisk som var ikke-medikamentelt behandlet sammenlignet med 33,9 ± 10,5 g/fisk som var medikamentelt behandlet. Syv dager med sulting i forkant av behandlingen førte til et ekstra tilveksttap på 155 g/fisk. I en merd med 150 000 fisk tilsvarte dette kortsiktige tilveksttapet en biomassereduksjon på 31 200 kg. Det betyr, at selv om perioden med sulting før behandlingen utgjør den største delen av tilveksttapet (~ 75%), viser resultatene i paper II at det også er viktig å inkludere det potensielle tilveksttapet etter behandlingen (~25%). Begge studiene viste betydelig variasjon både innenfor og mellom behandlingsmetodene, spesielt innenfor de ulike termiske behandlingene. Variasjon indikerer et potensial for forbedring hvis risikofaktorer for økt dødelighet og redusert vekst forbundet med behandlingsmetodene kan identifiseres og mitigeres. I paper II antydet resultatene at utfallet av en behandling primært påvirkes av faktorer som behandlingsrelaterte håndteringsprosedyrer, miljøforhold eller sykdomsstatus for fiskegruppen.

Videre indikerte resultatene en mulig forbedring av termisk behandling i perioden fra 2014 til 2019, da det ble observert en reduksjon i median dødelighet etter termisk behandling i løpet av denne perioden. Likevel er ikke-medikamentell behandling fortsatt ansett som en av de største helse- og velferdsutfordringene til oppdrettslaks. Både dødelighet i sjøfasen og bruken av ikke-medikamentelle behandlinger nådde sitt høyeste nivå i 2022.

Dødelighet og tapt tilvekst er en dyrehelse og velferdsutfordring og utgjør et biologisk tap. Omfanget av dette biologisk tapet ble implementert i en bioøkonomisk modell for å vurdere de økonomiske konsekvensene (kostnader og fordeler) det har for en oppdretter å velge ulike avlusingsregimer. Dette gjorde vi ved å bruke en stokastisk delbudsjett-tilnærming. Beregningene antydet at lakseprodusenter kunne investere en betydelig sum i tiltak for å forebygge eller forbedre termiske behandlinger før det ikke lengre var økonomisk lønnsomt. For eksempel kunne en oppdretter i gjennomsnitt bruke 5,4 millioner NOK/merd per 1-åringproduksjon på tiltak for å forebygge fire termiske behandlinger før det ikke lenger var økonomisk lønnsomt. Avhengig av utfallet av de fire termiske behandlingene kunne det brukes mellom 3,2 og 7,4 millioner NOK/merd per 1-åringproduksjon på tiltak for forbedring. Den bioøkonomiske modellen understreker viktigheten av å inkorporere risikoen for økt dødelighet og redusert vekst forbundet med ulike behandlinger, fordi når man gjør det, belyses også de økonomiske insentivene og behovet for å prioritere arbeidet med å forbedre metoder for å sikre god helse og velferd for oppdrettslaksen.

Arbeidet i denne doktorgraden viser at det er avgjørende å ta hensyn til de biologiske tapene forbundet med lusebehandlinger når man velger avlusingsstrategi. I årene som kommer, bør prinsippene for integrert skadedyrkontroll følges for å sikre en bærekraftig forvaltning av lakselus. Det betyr blant annet, at det er behov for å fortsette arbeid med å finne alternative løsninger både med tanke på kontroll og regulering av lakselus i Norge. Disse løsningene bør finnes gjennom tverrfaglig forskning og ved å veie alle de ulike aspektene lakselusen påvirker opp mot hverandre.

5 Synopsis

5.1 Introduction

When salmon farming in open net-cages was commercialised in the 1970s and the number of hosts increased rapidly in the following years, it did not take long for the salmon lice (*Lepeoptheirus salmonis* (Krøyer, 1837)) to become a pest. This is due to its reproduction strategy, which was originally evolved to few available hosts (salmonids), and a low probability of meeting these hosts (Pike & Wadsworth, 1999). The challenge with salmon lice affects the environment, economy, and society (Figure 1).

The spillover of salmon lice from farmed to wild salmonids is the main concern, as the parasite is regarded as a serious threat to wild stocks of sea trout (*Salmo trutta* L.), Arctic charr (*Salvelinus alpinus*), and Atlantic salmon (*Salmo salar*) smolts migrating through Norwegian fjords and coastal areas (Jackson et al., 2013; Krkošek et al., 2013; Thorstad et al., 2015; Torrissen et al., 2013; Vollset et al., 2018; Vollset et al., 2016b). Salmon lice control influences many parts of the on-growing production through regulation, surveillance, treatment, and prevention (Forskrift om kapasitetsjusteringer, 2022; Forskrift om lakselusbekjempelse, 2016; Produksjonsområdeforskriften, 2017). In recent years, the challenge with salmon lice has also become central to governmental regulation of the growth of salmon aquaculture (Produksjonsområdeforskriften, 2017).

Salmon farming has an important social impact by creating jobs and livelihood, and is important to many coastal communities in Norway (Torrissen et al., 2013). Salmon lice are a cost to the farmer due to lost biomass and treatment costs (Abolofia et al., 2017; Costello, 2009; Iversen et al., 2020; Iversen et al., 2017). In addition, negative publicity due to poor welfare of farmed salmon and cleaner fish may influence the public reputation of farmed salmon and the salmon industry. Negative environmental externalities such as salmon lice spillover to wild salmon, there is medicinal spillover harmful to non-target organisms, and increased carbon emission is a problem in itself and a cost to society (Asche et al., 2022; Torrissen et al., 2013). In 2015, a shift from medicinal to non-medicinal treatments occurred because of a widespread resistance to most of the pesticides previously used (Overton et al., 2018). This created a new problem, which was the negative impact of non-medicinal treatments on farmed salmon health and welfare (Overton et al., 2018). The impacts of delousing treatments on farmed salmon mortality and growth are the focus of this thesis.

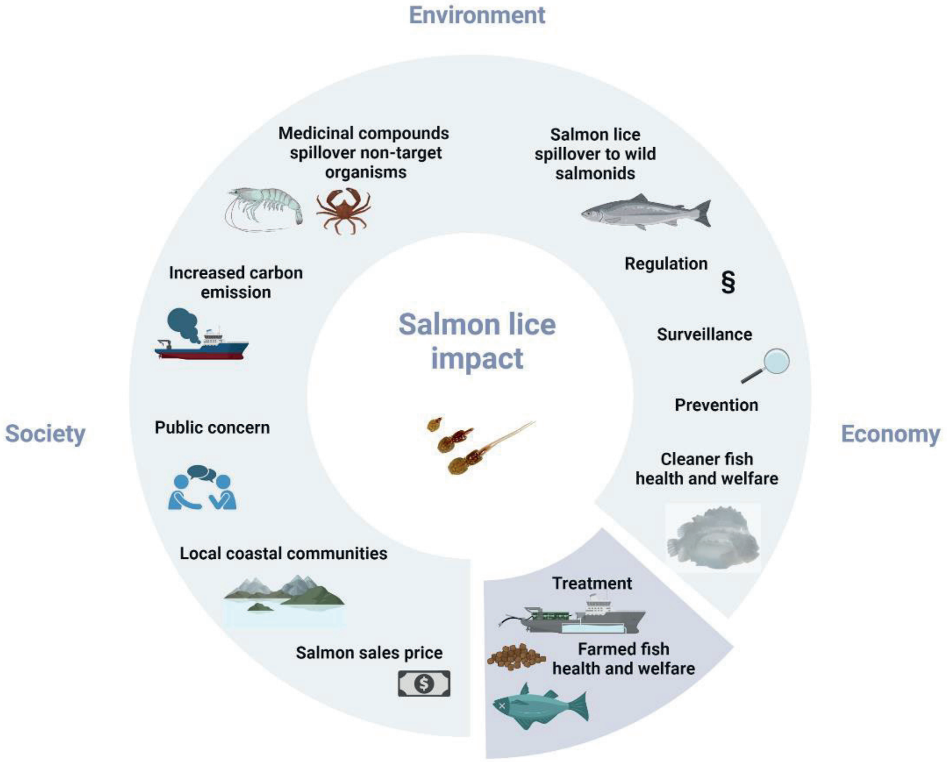

Figure 1. The different aspects that salmon lice affect. The darker shaded area is the focus of this thesis. Created with BioRender.com.

5.1.1 Salmon lice life cycle

Several species belongs to the family Caligidae, sea lice, where salmon lice is the primary species infecting the salmonid fish Atlantic salmon, sea trout, anadromous Arctic charr, and rainbow trout (*Oncorhynchus mykiss*) in the North Atlantic (Pike & Wadsworth, 1999).

Salmon lice is an obligate ectoparasite with a direct life cycle consisting of eight development stages (Hamre et al., 2013; Johnson & Albright, 1991a, 1991b) (Figure 2). The first two stages are planktonic nauplius larvae. The larvae moults into an infective copepodite that can attach to the skin of salmonids. If the parasite finds a suitable host, the last five stages develop on the salmon. These stages are divided into sessile (chalimus I and II) and later mobile pre-adult I and II and adult stages (Hamre et al., 2013; Johnson & Albright, 1991b).

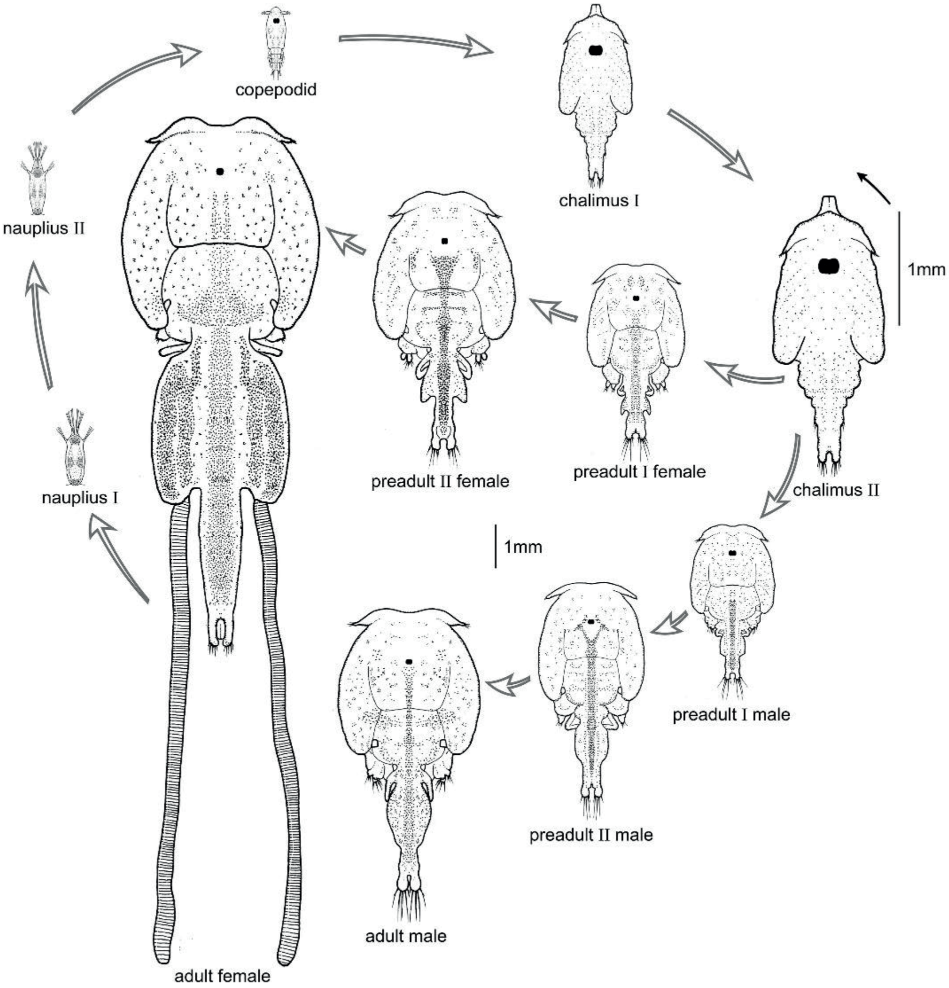

*Figure 2. Life cycle of the salmon louse (*Lepeophtheirus salmonis*), DataverseNO, V1 (Sea Lice Research Centre, 2020) CC0 1.0.*

5.1.2 Salmon lice dispersion

The number of lice, the number of eggs each female produces, the length of the pelagic life stages, the spatiotemporal variability of the ocean currents, and ocean temperature and salinity are major factors that influence the local infestation pressure of lice. Lice reproductive capacity is high. Each adult female louse produces batches of eggs within paired strings that can contain 300-600 eggs (Pike & Wadsworth, 1999). One female louse can produce between six to 11 pairs of egg strings (Hamre et al., 2009; Heuch et al., 2000).

Salmon lice will develop and reproduce faster with increasing seawater temperature up to 21 ^{0}C (Bjørn & Finstad, 1998; Finstad et al., 2000; Hamre et al., 2019; Heuch et al., 2000; Johnson & Albright, 1991a, 1991b; Stien et al., 2005; Tucker et al., 2000). The development from eggs to adult lice takes about 40 days at 10^{0}C (Johnson & Albright, 1991a, 1991b; Tucker et al., 2000; Wootten et al., 1982).

Figure 3. Female louse hatching nauplius larvae. With permission from Melanie Andrews.

The planktonic stages are mainly inert particles (Figure 3) that drift in the upper water current for up to tens of kilometres from the hatching source, depending on temperature and current (Johnsen et al., 2014; Samsing et al., 2015; Stien et al., 2005). The dispersion of planktonic stages is also affected by light (Heuch et al., 1995), swimming activity of the salmon (Heuch & Karlsen, 1997), and salinity (Bricknell et al., 2006; Heuch et al., 1995). The copepodite stages are typically in greatest abundance at shallow depths, beneath haloclines of 30 ppt in coastal waters (Heuch, 1995). The vertical distribution of copepodids seems to be controlled by light intensity, whilst the nauplii show only small differences in depth between night and day. The diel vertical migration pattern of the copepodid may increase the number of host parasite encounters since salmon will swim through populations of sinking (nighttime) and rising (dawn) parasites every 24 hours. Caged salmon feed at the surface during the day, and are therefore more likely to be exposed to infective copepodids compared to wild salmonids (Heuch et al., 1995). Salinity levels below 29 ppt severely compromise survival of both free-swimming and attached copepodid (Bricknell et al., 2006). The infestation success of the copepodid is correlated with temperature, where the highest success is at 10^0C (Dalvin et al., 2020).

A modest increase in the number of lice can lead to a massive change in the infestation pressure. If the number of adult female lice in a cage of 100 000 fish increases from 0.2 to 1.0 per fish, their infestation pressure can potentially increase up to 35 times (Marit Stormoen, personal communication, 12.05.2023). At a farm containing 1 million salmon, a seawater temperature of 12^0C and 0.5 adult female lice per fish, the number of eggs produced within a week could be about 250 million (Figure 4).

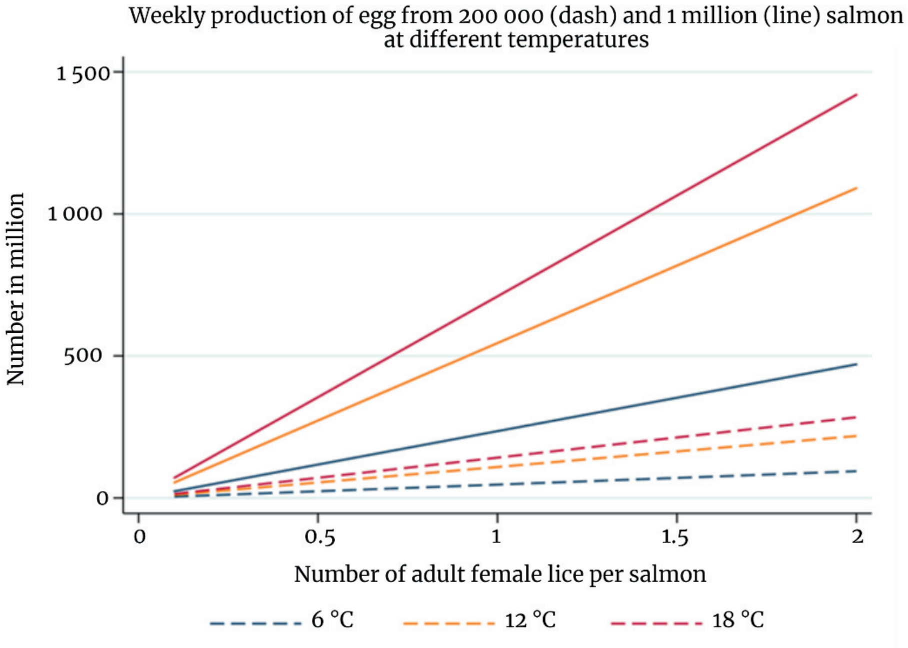

Figure 4. Graph showing the weekly production of eggs at different seawater temperatures when increasing the number of adult female lice. With permission from Marit Stormoen, Norwegian University of Life Sciences.

Mathematical models have been used extensively to aid management decisions and to understand the complex interactions between salmon lice, the salmon, and the environment (Groner et al., 2016). There exist several models to predict the infection pressure from farms and the spread of lice within and between farms in Norway; both hydrodynamic models (Asplin et al., 2020; Asplin et al., 2014; Sandvik et al., 2016) and statistical models (Aldrin et al., 2017; Aldrin et al., 2019; Aldrin et al., 2013; Kristoffersen et al., 2014; Stige et al., 2021). Both hydrodynamic and statistical models support decision making in the regulatory framework in Norway.

5.1.3 Host-parasite interaction

The severity of salmon lice infestation on an individual fish depends on infection intensity, developmental stage of the parasite, and size of the fish (Bjørn & Finstad, 1998). Even though large numbers of chalimus stages can cause severe stress, the pathology caused by salmon lice is mainly associated with the preadult and adult stages that feed on the mucus, skin, and blood of the host (Bowers et al., 2000; Finstad et al., 2000). If the infection levels increase beyond the salmon's ability to compensate, the parasite causes wounds, osmoregulatory dysfunction, physiological stress response, anaemia, reduced feeding and growth, and eventually death (Finstad et al., 2000; Grimnes & Jakobsen, 1996; Jones et al., 1990; Jónsdóttir et al., 1992). The current legal maximum limit of average of 0.2-0.5 adult female lice per fish per site (Forskrift om lakselusbekjempelse, 2016), is too low to cause the above mentioned problems for the farmed salmon (Bowers et al., 2000; Finstad et al., 2000; Grimnes & Jakobsen, 1996). However, the high reproduction potential of salmon lice has caused episodes of massive infestations in farmed salmon, which again leads to wounds and ultimately death (Hosteland, 2018).

5.1.4 The salmon lice challenge in aquaculture

Since the commercialisation of salmon farming, the challenge of salmon lice has been dealt with in different ways. This chapter gives a summary of the efforts made to control the lice through surveillance, treatment, and preventative measures, historically and in the present, starting with a brief overview of the production of Atlantic salmon in Norway.

5.1.4.1 Aquaculture of Atlantic salmon in Norway

The Food and Agriculture Organisation predicts that cultivated aquatic species will provide around 53% of the world's seafood supply by 2030 (FAO, 2020). Finfish farming has accounted for the largest share of world aquaculture for decades, and in 2020 farmed finfish reached 57.5 million tonnes. The main share comes from inland aquaculture (49.1 million tonnes), and the rest from mariculture in the sea and coastal aquaculture on the shore (8.3 million tonnes) (FAO, 2022). Norway's contribution to the world's marine production of finfish is substantial, and in 2022 Norway exported 1.2 million tonnes of salmon with a value of about 151 billion NOK (iLaks, 2023). In 2022, 337 million salmon were stocked at sea, and there were 989 active farms along the coast of Norway (Directorat of Fisheries, 2023a).

Commercial farming of salmonids was initiated in mid-Norway in the spring of 1970, and from there it developed rapidly from small-scale to a large-scale intensive production operated by multi-national companies (Asche et al., 2022). Figure 5 shows the increase in biomass (tonnes) of sold farmed Atlantic salmon in Norway from 1994-2021. The rapid growth of the Norwegian salmonid aquaculture is due to a number of innovations that have reduced production cost and improved competitiveness (Afewerki et al., 2023); they include breeding, improvements in feed, disease-control, vaccination, and control of smolt production. In addition, the increased scale of each farm (Asche et al., 2013) as well as a dynamic regulatory system have facilitated this growth (Hersoug, 2021).

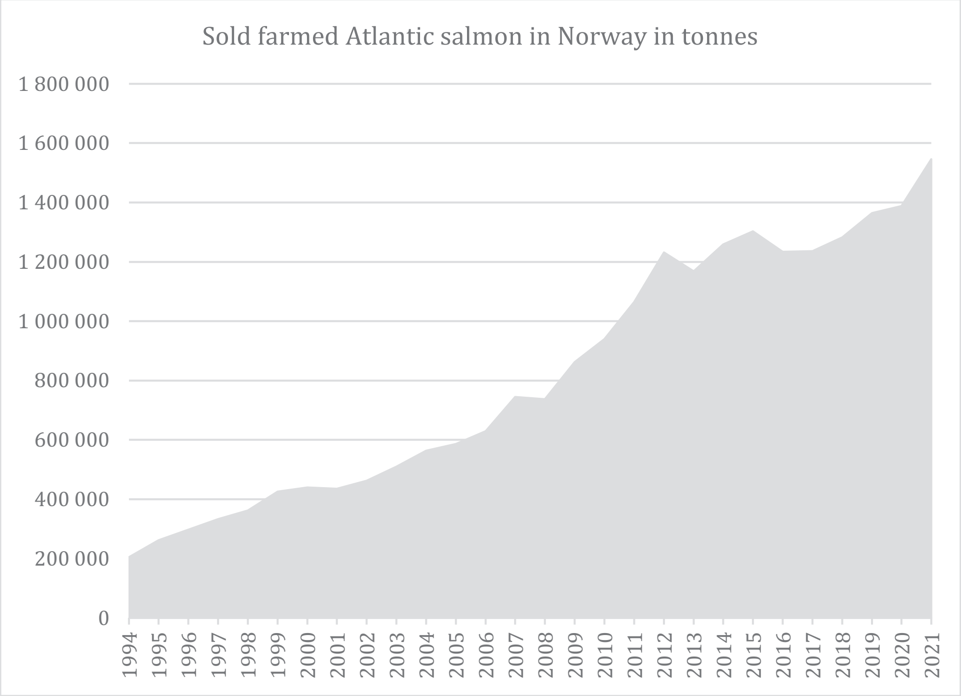

Figure 5. Increase in biomass of sold farmed Atlantic salmon in Norway from 1994-2021 in tonnes. Source: Directorate of Fisheries, 2023a.

Atlantic salmon are anadromous fish that spend the first part of their life in freshwater rivers. In the wild, salmon hide their eggs in river gravel. The egg hatches into a larvae called alevin (salmon sac fry) which further develops into a fry and later a parr. To be able to migrate to sea, the salmon adapts from fresh to saltwater by a physiological process called smoltification. The salmon can perform long-distance horizontal migrations at sea and spend several years in open sea before they return to the rivers again to spawn (Strøm et al., 2018).

Salmon aquaculture mimics the natural lifecycle of wild salmon (Figure 6). Production takes 2 ½-3 years from hatching of eggs until harvest (MOWI, 2022). In aquaculture settings, the fish spend the first 10-16 months of their life in a land-based freshwater facility. When becoming a smolt, they are transferred to sea either in the fall of the same year they hatched (0-yearling) or in the spring the year after they hatched (1-yearling), and will weigh about 100-250g (MOWI, 2022).

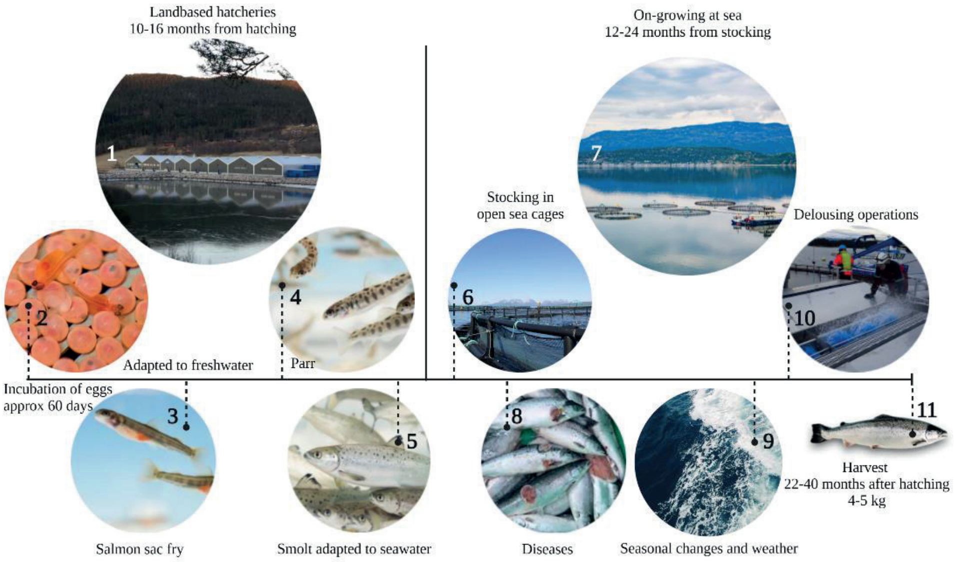

Figure 6. The production cycle of farmed Atlantic salmon and some important factors (8, 9 and 10) affecting mortality and growth in the on-growing period at sea. With permission from: 1. Britt Tørud, Norwegian Veterinary Institute, 2. Eivind Senneset, 3.-5 and 11. Norwegian Seafood Council, 6. Mari Press, Norwegian Veterinary Institute, 7. Colourbox, 8. Kristoffer Berglund Andreassen, Stim, 9. Thach Tran, Pexels, 10. Lena Vermedal, Alsaker Fjordbruk. Created with BioRender.com.

In the sea, they will spend their on-growing period in open net-cages for the remaining 12-24 months until harvest (MOWI, 2022). Salmon stocked in the same year is defined as a year class, and a generation is defined as fish stocked in either the spring or fall within the same year. The average harvest weight is 4-5 kg (MOWI, 2022). A marine farm is usually comprised of several cages, with a legal maximum limit of 200 000 fish per cage (Akvakulturdriftforskriften, 2008). Only one generation is allowed at the farm at a time, following the principles of 'all-in, all out'. Since the production time at sea is between 12-24 months, the fish will normally be stocked every second year at each farm.

Keeping track of the health of the farmed salmon, by registering mortality, daily weight gain, and growth rate, is an important part of the production. Norwegian aquaculture farming companies register daily production data concerning stocked fish, mortality numbers, feeding, environmental data etc. (Akvakulturdriftforskriften, 2008). The weight gain and growth rate in the production data systems are estimates, and companies can use several different models. The most important parameter when estimating daily weight gain is the amount of feed given to the fish. In Norway, salmon are fed by appetite and most farmers use underwater cameras to observe feeding behaviour, and stop feeding when the fish no longer eat. Appetite is evaluated by swimming behaviour and visible surplus feed pellets at a prior set water depth. Daily weight gain is estimated by the amount of feed given, the number of fish, and the biological feed conversion ratio (bFCR) per cage.

Since production at sea occurs in open net cages, the salmon are exposed to seasonal environmental changes such as fluctuating water temperatures, light, and salinity, in addition to different pathogens. Some of the most important diseases in the on-growing period are: viral diseases such as cardiomyopathy syndrome (CMS), heart and skeletal muscle inflammation (HSMI), pancreas disease (PD), and infectious salmon anaemia (ISA); and bacterial diseases caused by infections with bacteria such as *Moritella viscosa*, *Tenacibaculum* spp. and *Pasteurella* sp., in addition to complex gill disease (Sommerset et al., 2023).

Mortality in both the hatcheries (Gåsnes et al., 2021; Tørud et al., 2019) and on-growing period is high (Bang Jensen et al., 2020). For instance, in 2019, 53.2 million salmon, 16.1% of the standing stock, died in the on-growing period at sea. About eight million died after a catastrophic algae bloom in the northern part of the country, and 45 million died of other causes (Sommerset et al., 2020). The yearly mortality in the on-growing period at sea has been increasing since 2019 (Figure 7) (Sommerset et al., 2022; Sommerset et al., 2023).

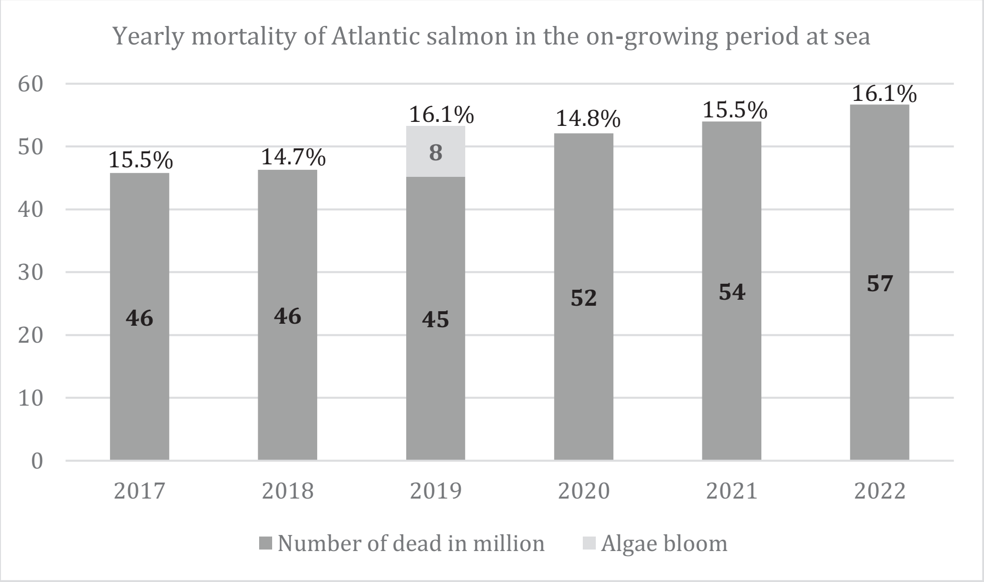

Figure 7. Yearly mortality of farmed Atlantic salmon in the on growing period at sea expressed as number of dead in million and as per cent of standing stock. Source: Sommerset et al., 2022; Sommerset et al., 2023.

5.1.4.2 Salmon lice surveillance

In 1997, the National action plan against salmon lice on salmonids was implemented in Norway with the long-term aim to reduce harmful effects of lice on farmed and wild fish to a minimum (Heuch et al., 2005). The national action plan introduced important measures such as legal limits for the maximum average number of lice allowed per farmed fish per farm, compulsory reporting of lice numbers to the government, strategic regional treatment against lice, and monitoring of salmon lice infection in wild salmonids (Heuch et al., 2005; Myksvoll et al., 2018). Strategic regional management includes coordinated stocking of single year-classes, fallowing of farms, and synchronised treatment strategies within fjords and between different aquaculture companies (Liu & Bjelland, 2014).

Currently, the legal maximum limit is average 0.5 adult female lice per fish per farm (NFD, 2012). This means that farmers need to keep the number of lice below this limit either by preventative measures or by treatments. The limit is lowered (to 0.2) in the spring and early summer to protect the migrating wild salmon (Forskrift om lakselusbekjempelse, 2016). Lice must be counted on 10-20 fish from all cages at a farm every week and reported to the government (Forskrift om lakselusbekjempelse, 2016). In addition, the farmer must report seawater temperature, treatment against salmon lice, type and amount of active substance used for treatment, results from sensitivity essays, and suspicion of resistance (Forskrift om lakselusbekjempelse, 2016).

5.1.4.3 Treatment of salmon lice

In the 1970s, organophosphates were introduced to control salmon lice infestations with good effect on lice removal (Brandal & Egidius, 1979; Burka et al., 1997; Burridge et al., 2010; Aaen et al., 2015). The use of pesticides allowed farms to treat salmon lice infestations without substantially reducing production. Until 2015, the use of pesticides was the preferred choice of keeping lice levels below the legal limit.

From the late 1970s to late 1990s, farmers applied in-cage bath treatment with organophosphates, first trichlorphon, then dichlorvos (Grave et al., 1991) and finaly azamethiphos in the early 1990s (Denholm et al., 2002). Azamethiphos was safer for farmers to handle, and there had been several episodes of high salmon mortality caused by lethal doses of trichlorphon (Horsberg et al., 1989; Salte et al., 1987). The organophosphates were later replaced by bath treatments with pyrethroids because of reduced sensitivity (Jones et al., 1992). Around 2000, reports of treatment failure with pyrethroids were registered in Norway (Sevatdal & Horsberg, 2003). The pyrethroids were subsequently replaced by hydrogen peroxide baths and later emamectin benzoate and flubenzurones (Denholm et al., 2002). From 2000 and onwards, emamectin benzoate was the dominating pesticide used. When problems with resistance against emamectine benzoate arose around 2008-2009 (Espedal et al., 2013), there were no novel compounds available. Thus, the use of organophosphates, pyretroids, and hydrogen peroxide were reintroduced. The initial effect was good, but problems with resistance reappeared quickly (Fjørtoft et al., 2021).

In addition, concerns were raised about the negative externality of spillover of medicinal compounds potentially harmful for the non-target aquatic crustaceans (Burridge et al., 2010) such as crab larvae (Gebauer et al., 2017), shrimp, and lobster (Burridge et al., 2014; Parsons et al., 2020). To minimise the medicinal spillover and suboptimal treatment effects when treating in skirts (Nilsen et al., 2010a; Nilsen et al., 2008), the use of a full tarpaulin around the cage was required in bath treatments of salmon around 2006, with a subsequent transition to treating in well-boats.

The challenge with resistance forced a paradigm shift from medicinally to non-medicinally treating (Figure 8). Treatments at farm level are reported weekly to the authorities, which means one treatment week can cover treatment of one, several or all cages at a farm. There is no publically available data describing how many times one fish-group is treated during the production at sea. Non-medicinal treatments can be grouped into thermal or mechanical delousing methods, with the use of freshwater baths as an independent delousing procedure or as a supplement to the thermal and mechanical methods. Thermal treatments were introduced around 2014 and, by 2016, these, together with mechanical treatments, had largely replaced medicinal treatments (Helgesen et al., 2023; Overton et al., 2018). Since then, thermal treatment has been the most frequently applied method for removal of lice in Norway (Helgesen et al., 2023). The principle of thermal treatment is to inactivate the lice by exposing salmon with lice to heated water (28-34°C) for 20-30 seconds (Holan et al., 2017; Noble et al., 2018). The sudden increase in water temperature causes the lice to detach from the fish, and the lice are removed by filtration of the treatment water (Grøntvedt et al., 2015; Roth, 2016). Thermal treatment is shown to be effective in removing pre-adult and adult salmon lice (Grøntvedt et al., 2015; Roth, 2016). However, physical injuries were early on observed on the treated fish (Grøntvedt et al., 2015; Roth, 2016). In mechanical delousing, the lice are removed by either water jets, or flushing and brushing (Erikson et al., 2018; Gismervik et al., 2017; Nilsen et al., 2010b). Mechanical treatment is shown to have a good effect in removing adult lice, but varying effect on the farmed salmons' health and welfare (Gismervik et al., 2017; Nilsen et al., 2010b). Freshwater treatment against salmon lice and amoebic gill disease (AGD) involves bathing the fish in low salinity water to inactivate the parasite (Powell et al., 2015).

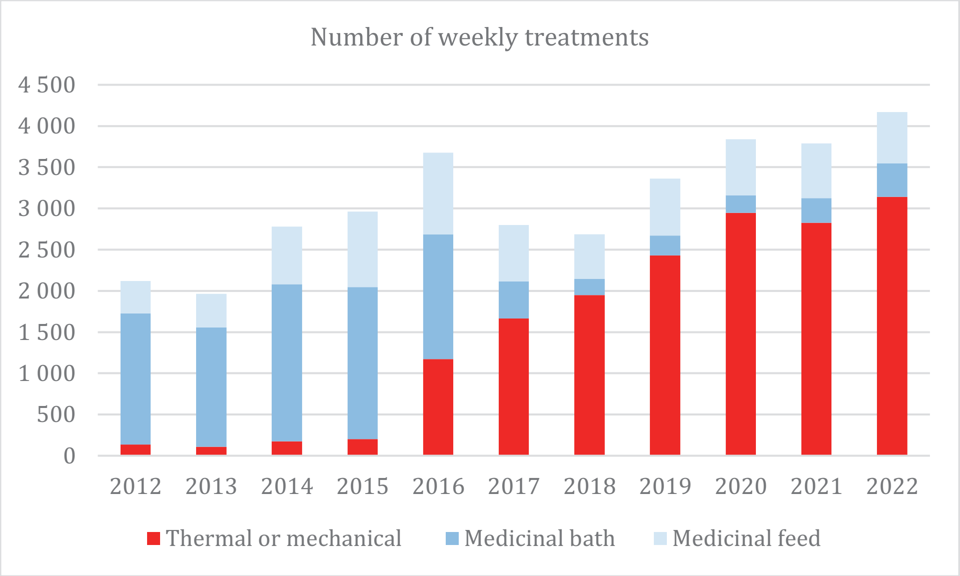

Figure 8. Total number of weeks farms have reported treatments of salmon lice (treatment weeks), in the mandatory salmon lice report to the Norwegian Food Safety Authority from 2012-2022. Treatments are reported at farm level; however, one 'treatment week' may be treatment of one, several, or all cages at the farm. Based on official records and retrieved from barentswatch.no.

Thermal, mechanical, and freshwater treatments are performed in well-boats or in treatment chambers in specialised rigs, which requires crowding and pumping of the fish. Crowding the fish is needed regardless of treatment type. Thus, handling the fish by crowding and pumping is an inherent part of the non-medicinal and medicinal treatment performed in well-boats. In the following link, one can see the extent of thermally treating one cage: https://www.youtube.com/watch?v=A-4tUnXhdzY (Optimar, October 23th 2020). Since all treatments are performed in closed compartments (being either a well-boat, treatment chamber, or tarp around the cage), there is a risk of the water quality deteriorating when the water volume and water exchange is reduced. To reduce the risk of reduced water quality, salmon are starved prior to treatment to minimise the amount of faeces during the operation (Einen et al., 1998). The number of days of starvation is determined by seawater temperature, size, and health of the fish (Anonymous, 2020)

Not long after the large-scale implementation of the non-medicinal treatments, veterinarians working in the field raised concerns about thermal and mechanical treatments being harsh on the fish as injuries and wounds were observed on treated fish. In addition, episodes of high post-treatment mortality were reported (Hjeltnes et al., 2018). About five years after the introduction of these methods, it was reported that the most important problem in the on-growing period at sea was mechanical injuries after non-medicinal treatments (Sommerset et al., 2020).

5.1.4.4 Prevention

In addition to the shift to non-medical treatments, the use of preventive measures has become more relevant in recent years. Currently, an array of different preventive measures exists, and Barrett et al. (2020a) give an extensive review. Normally the farmer will use a mixture of preventive measures in addition to treatments (Oldham et al., 2023).

A skirt around the cage is one of the most applied preventive measures (Stien et al., 2018). These skirts are strapped around the cages to block particles in the upper part of the water column from entering the cage, and vary in depth (5-10m) and material (tarpaulin, canvas, or plankton sheeting) (Stien et al., 2018). Another sea cage barrier design is a fully enclosed cage which consists of an impermeable tarpaulin with a water intake depth of about 25m (a depth regarded as low risk of encountering the copepodid stage) (Nilsen et al., 2020; Nilsen et al., 2017). Farmers can also manipulate the swimming depth of the salmon, below the depth at which the lice are most abundant, by the use of deep feeding or light (Frenzl et al., 2014), by 'snorkel' lice barrier technology (Geitung et al., 2019; Oppedal et al., 2019; Oppedal et al., 2017; Stien et al., 2016; Wright et al., 2017) or submerged cages with air domes (Sievers et al., 2022). Other measures of prevention that are available or in the making are filtering and trapping, repellents and host cue masking, incapacitation, vaccines, and breeding. The effect of these other measures are described in detail in Barrett et al., 2020a, but most of them have not succeeded in sufficient lice control.

The problem of salmon lice, and other pathogens harmful to the salmon in the on-growing period, have affected the traditional strategy of producing 0- and 1-yearlings (Ytrestøyl, 2022). Some companies reduce the number of delousing operations by stocking open sea cages with post-smolts that are 1 to 1.5 kg (Ytrestøyl, 2022).

The use of cleaner fish has been and still is widely applied as a biological control or continuous measure of delousing salmonids (Erkinharju et al., 2021). Cleaner fish consist of lump suckers (*Cyclopterus lumpus* L.) and different species of European wrasse (Labridae) such as ballan wrasse (*Labrus bergylta* Ascanius), gold-sinny wrasse (*Ctenolabrus rupestris* L), and corkwing wrasse (*Symphodus melops* L.) (Erkinharju et al., 2021). In the wild, cleaning activity is a form of symbiosis between two species, where one cleans the other of ectoparasites and dead tissue. Unlike 'true' cleaner fish, the cleaner fish used as a biological pest control against salmon lice in salmon farming are opportunistic cleaners (Vaughan et al., 2017). This means they need to adapt to the sea cage environment and learn to approach and clean salmon (Overton et al., 2020). Problems with diseases, lack of adaptations to the needs and requirements of wrasse and lumpfish, and high levels of mortality have raised great concerns about the use of cleaner fish (Brooker et al., 2018; Erkinharju et al., 2021; Nilsen et al., 2014; Norwegian Food Safety Authority, 2020). The number of stocked cleaner fish increased rapidly from 2012 and reached a maximum when about 60.9 million cleaner fish was stocked at sea in 2019 (Sommerset et al., 2020) (Figure 9). It is shown that the delousing effect of cleaner fish is highly variable (Barrett et al., 2020b) and a recent review by Overton et al. (2020) concluded that there is a mismatch between the current evidence of effect and the extent of use by the industry. The number of stocked cleaner fish was reduced to 45.5 million in 2022, probably as a consequence of this.

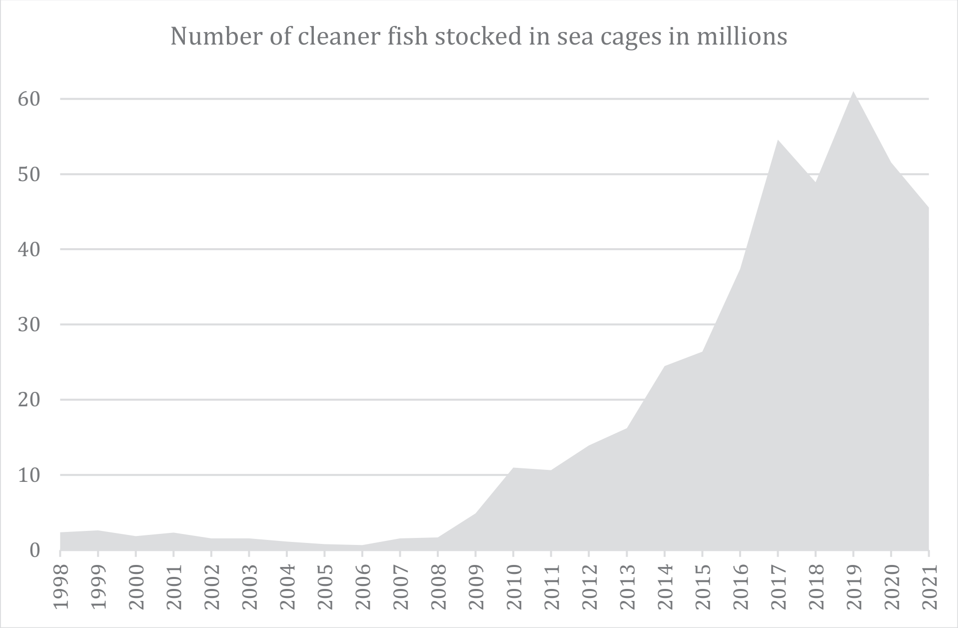

Figure 9. Number of cleaner fish stocked in sea cages in the period 1998-2021. Source: Directorate of Fisheries, 2023b.

5.1.4.5 Regulation

In 2017, the Norwegian government ratified a management system called 'the traffic light system' to secure a sustainable growth of the industry (Produksjonsområdeforskriften, 2017). The Norwegian coast was divided into 13 different production areas (Ådlandsvik, 2015), and the environmental sustainability within each area is the governing principle for management decisions. The environmental impact of fish farming within each area should be evaluated by several different factors, and effects of salmon lice on wild salmonid mortality was the first implemented indicator of the environmental sustainability of an area. (Vollset et al., 2018). No new sustainability indicators have been introduced since the implementation of the traffic light system in 2017. Salmon lice therefore ended up having a huge impact on the regulation of the growth of salmonid aquaculture in Norway.

To calculate the effect of salmon lice on wild salmonid mortality, results from the national surveillance program is used as input in three different lice-distribution models combined with models predicting migration of wild salmonids. The results are calibrated against the lice infestation levels observed on wild fish in the surveillance program. The spatial distribution of lice is calculated by explicit spatially statistical models (Aldrin et al., 2013; Jansen et al., 2012; Stige et al., 2021) and hydrodynamic models (Asplin et al., 2014; Johnsen et al., 2014; Sandvik et al., 2016), in addition to models predicting the spatiotemporal distributions of different salmonid species within fjord and coastal waters (Finstad et al., 2005; Thorstad et al., 2012; Vollset et al., 2016a; Økland et al., 2006). The levels of sea lice on wild fish is compared with threshold levels of mortality to determine how much of the population is expected to die due to sea lice (Taranger et al., 2014). Based on this information, the production area will be given a green, yellow, or red light every second year if 0-10%, 10-30% or >30% of the sea migrating smolts are likely to die because of sea lice infestation, respectively. If assessed as green, yellow, or red, the production volume (biomass) within the area can increase, maintain at current volume, or decrease, respectively.

5.1.5 The economic impact of the salmon lice challenge

Many diseases are detrimental to salmon aquaculture production as they reduce growth rates and, in worst case, induce mortality, thereby reducing health and welfare, increasing production cost, and reducing profitability (Iversen et al., 2020). However, production losses also create economic incentives to prevent or treat the diseases, and increased knowledge of disease interventions has improved the industry's ability to do so (Afewerki et al., 2023).

Several studies have shown the enormous monetary costs associated with salmon lice both in Norway and globally, and thus highlighted the importance of prioritising the problem at a macro- and microeconomic level (Abolofia et al., 2017; Costello, 2009; Iversen et al., 2020; Liu & Bjelland, 2014; Mustafa et al., 2001; Olaussen et al., 2015). The total cost of salmon lice control in Norway was estimated at 8.7% of the Norwegian industry`s total value in 2011 (Abolofia et al., 2017). Still, new problems have replaced some of the old ones since 2011, especially the shift from medicinal to non-medicinal treatments which involved increased costs due to large investments in specialised treatments rigs and added costs of biomass loss associated with the treatments. In 2017, the cost of managing salmon lice, including the use of non-medicinal treatments, was estimated at NOK 5 billion per year (Iversen et al., 2017).

However, the estimated cost of the biomass loss associated with especially non-medicinal treatments was crude and based on expert opinion, as information on this matter did not exist.

5.1.6 Knowledge gaps

In 2020, 52 million salmon died during the on-growing period at sea, which was about 16% of the standing stock (Figure 7) (Sommerset et al., 2021). This was even higher compared to the previous year, and there were no single events such as the algae bloom to explain why. The high mortality in the on-growing phase is most certainly multifactorial, and prevalence of many different diseases is an important factor explaining this mortality. Still, in 2020, the main reason for reduced animal health and welfare in the on-growing period at sea was pointed out by veterinarians working in the field as the non-medicinal treatments against salmon lice (Sommerset et al., 2021). Since the large scale implementation of the non-medicinal treatments in 2015, veterinarians have expressed serious concerns about these treatments not ensuring good health and welfare of the salmon (Hjeltnes et al., 2018; Hjeltnes et al., 2019; Sommerset et al., 2021; Sommerset et al., 2020). At the onset of this PhD, we had insufficient knowledge of how many salmon died after these treatments. Further, we did not know how these treatments affected salmon growth. We suspected that the fish which survived non-medicinal treatment would be stressed for some period of time afterwards, and this would cause an appetite drop (Folkedal et al., 2012). In addition to the pre-treatment starvation period, suboptimal feeding after treatment could be an important contributor to treatment-associated biomass loss. If the biomass loss was underestimated, the cost of delousing operations would also be underestimated. In addition, since we lacked information on how much mortality and growth loss associated with a specific treatment method varied, we could not assess how much could be spent on reducing these losses by improving treatment methods.

Securing good health and welfare is part of sustainable animal production and should be a top priority. Yet, when we do not know the extent of mortality and growth loss associated with delousing treatments, it is difficult to assess how much could be spent on measures to reduce mortality and secure good growth. Consequently, it is also difficult to evaluate how highly work on reducing mortality and securing good growth after treatment should be prioritised.

5.1.7 Aims and objectives

The overall aim of the thesis was to assess the biological and economic impact of delousing farmed Atlantic salmon in Norway. To achieve the overall aim and address the identified knowledge gaps, the following objectives were formulated:

Objectives:

1) Describe the extent of mortality and growth loss associated with different delousing operations of farmed Atlantic salmon in Norway (papers I and II).
2) Analyse the direct effect of different delousing operations on the growth of Atlantic salmon in Norway (paper II).
3) Assess the economic consequences for a farmer of choosing between different delousing regimes (paper III).

5.2 Materials, methods, and methodological considerations

5.2.1 Study design

With the first and second objectives, we wanted to evaluate the biological losses associated with different delousing operations (exposure). The biological losses are defined as increased mortality and decreased growth (outcomes). To solve these two objectives, we gathered data describing daily production at cage level in 2014-2019 from three large Norwegian aquaculture companies, and performed two retrospective observational studies following different fish-groups of Atlantic salmon in a period before and after salmon lice treatment (longitudinal cohort study). The study on mortality (paper I) was a descriptive study, where we estimated mortality distributions at cage-level, using mortality rates. In the study of growth (paper II), we evaluated the direct (short-term) effect of delousing operations on the growth of salmon, using a linear mixed effect model. In this study, we applied the thermal growth coefficient (TGC), to measure growth.

To solve the third objective, we built a biological model simulating production cycles with and without delousing treatments. We incorporated the risk of biological losses associated with different delousing treatments using Monte Carlo simulation. The outputs from the biological model were applied as inputs in an economic scenario model to assess the economics of preventing, replacing, or improving different delousing treatment regimes using a partial budgeting approach (paper III).

5.2.2 Data

The first two objectives were to estimate the biological losses associated with delousing methods. Thus, we needed to sample enough data to evaluate a possible association between treatment and the extent of biological losses, and to be able to detect differences in outcome between different delousing methods. This required daily production data on cage (fish-group) level, and data of such high resolution is not publicly available.

We asked five large aquaculture companies (companies with >20 farms) for daily production data. Three provided data. Since we wanted to compare medicinal to non-medicinal treatments, we decided to start the study period with salmon stocked in spring 2014, as the shift from medicinal to non-medicinal happened in 2015-2016. Sampling of data started in 2019, thus the study period ended with fish-groups being harvested in the fall of 2019. The received data described cage-level production of four year-classes of farmed Atlantic salmon stocked at sea at 210 farms. Of these, 85 produced more than one generation of fish during the study period. A fish-group is defined as a group of fish stocked in the same cage at the same time. The dataset covered production areas 1-9 and 11, with the main share in 3-7 (84%). The source population (Dohoo et al., 2014e; Ersbøll et al., 2004) is thus Atlantic salmon in the on-growing phase at sea, farmed by three large Norwegian salmonid farming companies operating in multiple production zones along the Norwegian coast. During the study period, there were 717 active farms along the coast (Oliveira et al., 2021), thus the source population represented about 29.3 % of the entire production of farmed Atlantic salmon in Norway.

We applied the same source population for all three studies described in papers I-III. However, due to different inclusion criteria, the study population in paper I and II are not identical. Two of the companies supplied daily production data. The third company delivered accumulated production data related to a salmon lice treatment. This dataset described the mortality of a fish-group seven days before a treatment, and in a period of one, seven, and 14 days after a treatment. These three datasets were merged, managed, and applied in paper I. The accumulated dataset from the one company was later replaced with daily production data from the same company within the same study period to enable tracing of cohorts from stocking at sea until harvest, and calculate growth. This dataset, in addition to the other two datasets describing daily production, were applied in paper II.

In the dataset applied in paper I, one row corresponded to one delousing treatment of one fish-group. Before data management and exclusion, the dataset consisted of 6 131 delousing treatments of four year-classes of Atlantic salmon in 210 farms during 2014-2019. After data management and exclusion as described in the paper, the dataset consisted of 4 644 delousing treatments in 159 farms in 1 837 fish-groups consisting of about 24.7 billion Atlantic salmon. The first delousing occurred in May 2014 and the last in April 2019.

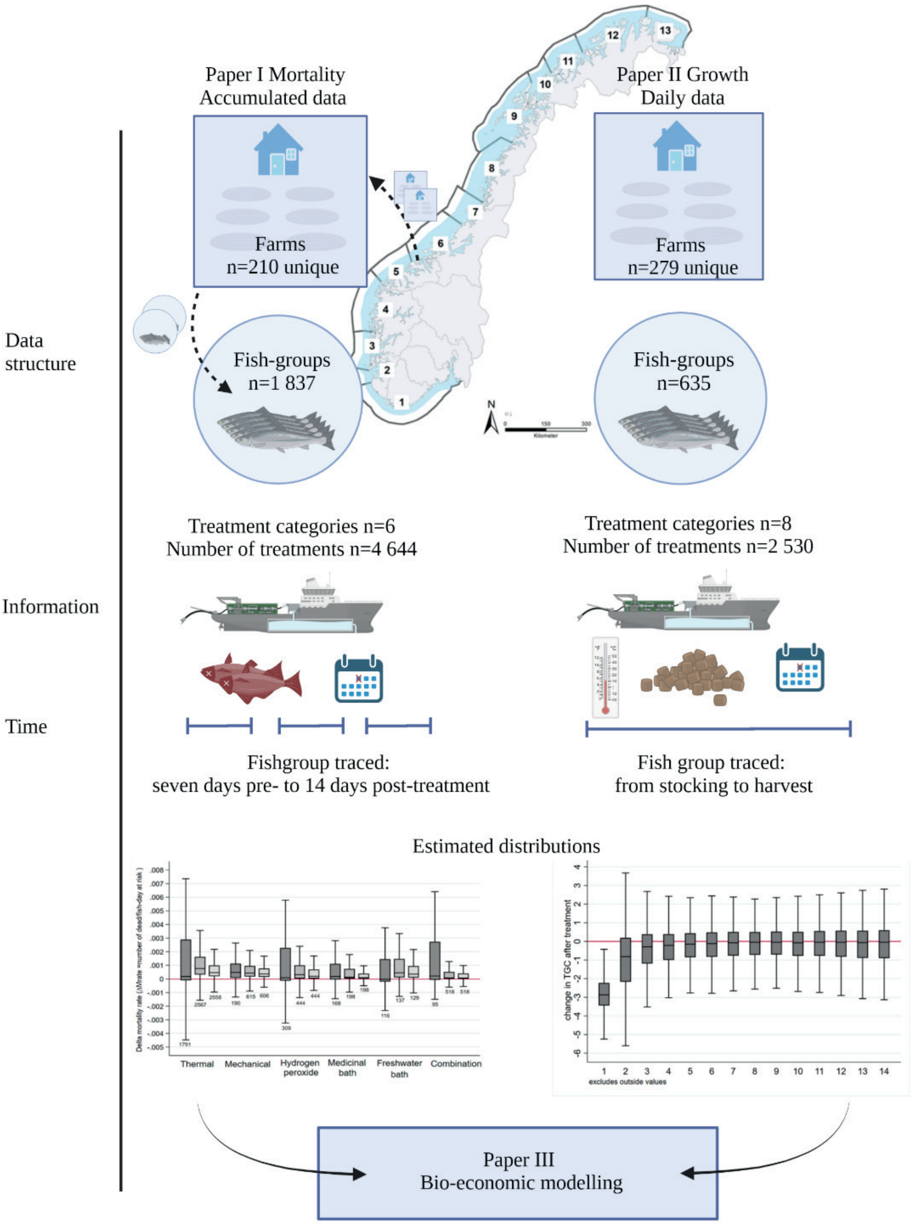

Figure 10. Overview of data applied in the three different papers. Fish-groups are clustered within a generation, within a farm, within a production area. The production areas are marked 1-13 in the map of Norway. Information on treatment date, number of dead, seawater temperature, feed amount, and time period the fish-groups were traced in papers I and II. The estimated distribution from these two papers were included in paper III. Created with BioRender.com.

In the dataset applied in paper II, one row corresponded to one production day of one fish-group. The dataset consisted of 1 022 472 observations prior to exclusion. After data management and exclusion as described in the paper, the dataset consisted of 306 855 observations, from 97 farms and 124 production cycles. In total, 635 fish-groups were treated 2 530 times. An overview of the data applied in papers I-III is shown in Figure 10.

5.2.3 Tracing fish-groups

A key to understanding the dynamics of biological losses is the possibility to follow the same fish-group before and after a treatment. At the time of stocking, the different groups of fish are usually designated a unique number in the production data. In more recent production data, this number serves as a consistent identification number throughout the entire production period, making it possible to track the same fish-group from stocking at sea to harvesting, thus investigating the temporal order of events. However, in the study datasets describing daily production, several fish-groups did not hold a consistent identification number.

When fish-groups are deloused, they are often transferred from one cage to another. Occasionally, groups of fish are also split between cages, or merged with other fish-groups. In addition, a fish-group might be partially harvested at the end of the production cycle. Each time a transfer of fish-groups occurred, the designated identification number in the production data also changed. In such cases, the high resolution of the daily production data often made it possible to detect and trace fish-groups by comparing estimated average weight and number of fish in each cage before and after transfer. Occasionally, there were movements of several groups of fish with approximately equal weights and numbers to different cages on the same day, or adjustment of weight and number in a group during handling or transfer. As a result, the weight and number before and after movement between cages was not always identical. Therefore, we cannot dismiss the possibility that some fish-groups were not correctly traced. In several cases, it was not possible to trace fish-groups from stocking to harvesting, and this is the main reason why many fish-groups had to be excluded in paper II.

5.2.4 Delousing treatments

The main variable of interest was treatment method against salmon lice. The production data included information on the date of treatment, cause for treatment, treatment method, and active substance for medicinal treatments. Based on this information, delousing treatments were divided into different categories as presented in Table 1. As the production data contained detailed recordings of the delousing operations, possible bias of misclassification of the methods is evaluated to be low. It was not possible to categorise delousing as treatment in cage or well boat, as recording of this information was not consistent.

We did not expect that delousing with medicinal feed would give increased mortality (Veterinærkatalogen, 2022b); therefore treatment with medicinal feed was not included.

Both freshwater and hydrogen peroxide are applied to remove the causative agent for the disease amoebic gill disease (AGD), *Paramoeba perurans,* in addition to salmon lice. Hydrogen peroxide and freshwater treatment against both AGD and salmon lice were included in papers I-III. Hydrogen peroxide and freshwater treatment against only AGD was excluded in paper I, but included in paper II, since there it was possible to investigate the temporal order of events, and excluding AGD-treatment could bias the results. Hydrogen peroxide and freshwater treatments against AGD differ in holding time and concentration (Holan et al., 2017; Hytterød et al., 2017; Veterinærkatalogen, 2022a). Therefore, treatment against only AGD was categorised separately based on treatment indication.

Table 1: Categories (n=8) of delousing treatments applied in farmed Atlantic salmon in three Norwegian companies from 2014-2019 included in papers I-III.

Categories of treatment operations	**Description of category of delousing operation**	**Included in paper**
Thermal	Non-medicinal treatment using heated seawater. Includes all treatments using: a. Optilice ® b. Thermolicer c. Heated seawater	I, II and III
Mechanical	Non-medicinal treatment using brushing or flushing. Includes all treatments using: a. FLS Avlusersystem b. Hydrolicer c. SkaMik d. Flushing or mechanical treatment	I, II and III
Hydrogen peroxide	Hydrogen peroxide (H2O2) bath in pen or well boat against salmon lice	I, II and III
Medicinal bath	Medicinal bath in pen or well boat using one of the following active substances: a. Azametiphos b. Cypermethrin c. Deltamethrin d. Imidaclorid e. Other	I, II and III
Freshwater bath	Freshwater bath in pen or well boat against salmon lice	I, II and III
Combination medicinal	Treatment of the same cohort with two different delousing methods on the same day. Includes the following combinations: a. two different active substances b. hydrogen peroxide and medicinal bath	I, II and III
Hydrogen peroxide AGD	Hydrogen peroxide (H2O2) bath in pen or well boat to treat amoebic gill disease (AGD)	II
Freshwater AGD	Freshwater bath in pen or well to treat amoebic gill disease	II

5.2.5 Estimating mortality and growth

To calculate mortality in paper I, we used an incident rate expressed as the mortality rate. Using an incident rate makes it possible to compare populations where animals may leave or enter for other reasons than death (open population). In the data provided, we could have calculated the exact time at risk in the datasets describing daily production since we had the exact date of death. However, to simplify the work of computing animal time at risk, we chose to assume that the animals died uniformly during one week before, and one and two weeks after, treatment. This assumption is reasonable as the sample size in this study is large (Toft et al., 2004). An incident rate is not an intuitive number, mainly because it operates with the term 'animal time at risk'; thus we recalculated the incident rate as an incident risk.

When estimating the growth rate of salmon, we used one of the most commonly applied formulae: the thermal growth coefficient (TGC), that adjusts for both temperature and size of fish (Cho, 1990; Iwama & Tautz, 1981). However, it does not adjust for the effect of light (mean day length and twilight) and latitude on growth (Aunsmo et al., 2014). TGC will give spurious results for fish experiencing marked changes in body condition, and temperatures outside the range of 7.5-12.5^{0}C (Jobling, 2003). The main share of the observations in the dataset were within this temperature range.

5.2.6 Statistical analysis

A spatial and a temporal clustering arises from the dataset because the fish-groups share common features. Groups of fish are clustered within a generation (year-class) within a farm within a production area (Figure 10). However, there is also a temporal clustering as groups are usually treated within the same week. In addition, most of the fish-groups had the same number of previous treatments. Even though the dataset was large, we had to omit production area and year-class as clusters (random effects) in paper II because there were too few production cycles within a farm and the variance of number of farms within a production area was too high.

Clustering can lead to dependences between the responses of observations in a group, violating the conditional independence assumption in linear regression

(Dohoo et al., 2014c; Rabe-Hesketh & Skrondal, 2008). Mixed effect modelling is regarded as an appropriate method to deal with this problem (Dohoo et al., 2014c, 2014d). Mixed models are also known as variance component models because the variance in the dataset is decomposed into defined clusters (Dohoo et al., 2014d); in our case, fish-groups within a farm. This makes it possible to identify at which level most of the variance lies, thus indicating where it would be reasonable to start testing risk factors.

5.2.7 Stochastic partial budgeting

Partial budgeting is a well-known economic tool to support decision-making processes in different areas of animal production (Rushton, 2009a) and has also been applied in salmon production (Aunsmo et al., 2010; Pettersen et al., 2015). This tool quantifies the economic consequences of a specific change in the production procedure by comparing the negative and positive impacts to find the economic net benefit of the change. Thus, a partial budgeting analysis does not describe the profitability of a production cycle, but rather how profits are affected by, for instance, choosing one delousing method over another. Therefore, only variables that will change if another alternative is chosen should be included in the analysis. The strength of a partial budget approach lies in the comparison of alternative uses of resources in a structural manner. A partial budgeting approach is a sensible choice when comparing the monetary cost and benefits of different delousing operations (third objective). The analysis is further strengthened if including the variation in mortality and decreased growth associated with different delousing methods, such that the expected monetary outcome and associated risk of biological loss using different delousing treatments, can be calculated.

The mortality and growth associated with different delousing methods were incorporated in a production model (Figure 11) to provide input on the biological loss in the partial budget model described in paper III. The biological input variables time of stocking, number of stocked within a fish-group, weight at stocking, number of days from stocking to harvesting, growth rate between treatments, treatment month, number of days between treatments, and seasonal changes in temperature were based on distributions from the two datasets described in papers I and II. The production model was built in Microsoft ® Office Excel. We applied a Monte Carlo simulation of the estimated distribution of mortality and growth, by using the program @Risk (Lumivero). The distributions for the stochastic variables were fitted by the function distribution fit in @Risk, and the distribution with the highest Akaike information criterion (AIC) was chosen. The biological output variables from the simulated production cycles and economic input variables, described in paper III, were applied to calculate the monetary impacts of changing a treatment regime. The main output of interest was the economic net benefit of a scenario, expressed as the change in profit.

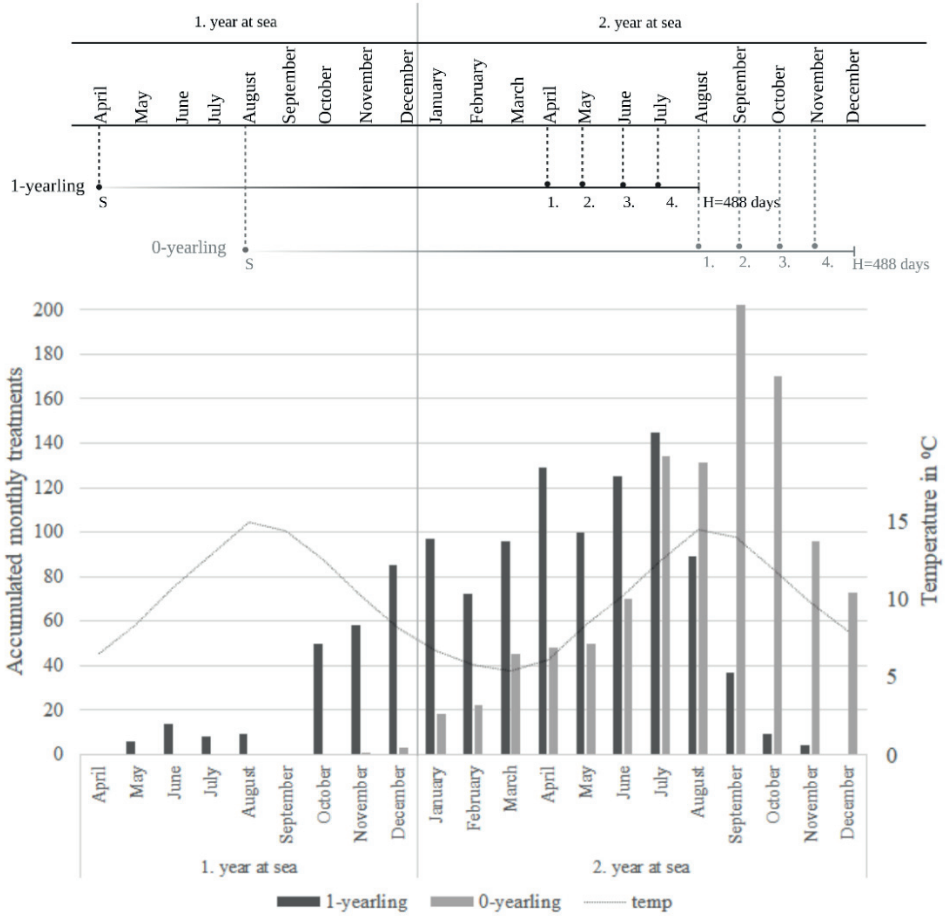

Figure 11. The modelled production cycle of the two smolt groups with month of stocking (S), treatment month (numbered 1 to 4), and month of harvest (H). The monthly occurrence of treatments (table graph), and the seasonal changes in mean temperature (^0C) (dotted line) from the dataset were incorporated in the model.

5.2.8 Methodological considerations

"That's right," shouted Vroomfondel, "we demand rigidly defined areas of doubt and uncertainty!"

-Douglas Adams, *The Hitchhiker's Guide to the Galaxy*, 1979

Observational studies observe the state of the world without manipulating it, and therefore it is argued that these studies may have less power to detect causal relationships compared to experimental studies or randomised clinical trials (Dohoo et al., 2014b). Even though longitudinal cohort studies present some unique challenges, they should be considered when randomised clinical trials are not possible due to practical, ethical, logistical, or financial reasons (Dohoo et al., 2014a). In our case, it would be difficult and costly to mimic a real life delousing treatment in controlled settings. The longitudinal cohort study design was chosen to calculate the association between delousing operations and mortality and growth of the farmed salmon. Using existing production data is a cost-efficient way of performing a longitudinal cohort study. When properly designed and interpreted, links between exposures and outcomes (including an indication of causality) can be made (Dohoo et al., 2014a). The validity of observational studies depends on the extent of systematic and random errors.

5.2.8.1 Systematic errors

A systematic error arises when a feature of a study leads us to obtain an estimate that is not equal to the population value. Increasing the sample size will not reduce the magnitude of this type of error (Dohoo, 2014). There are three main types of bias which generate systematic errors: confounding, selection bias, and information bias (Dohoo, 2014).

In a cohort study, the frequency of the outcome in two groups that are similar in all regards except for the exposure, is compared. The quality of the study results will depend on how closely the real study comes to that ideal (Dohoo et al., 2014a). In our case, finding a suitable, untreated group that was similar to the treated group in all regards expect for the exposure was challenging, because we had the problem of systematic errors arising from especially unmeasured variables (confounders) that were not recorded or inconsistently recorded in the production data. Examples of such unmeasured confounders were occurrence of disease, seasonal variations, breed, management factors (crowding time, handling time etc.), and environmental differences (light, longitude, water quality etc.).

In the dataset, normally all cages (fish-groups) at a farm were treated within the same week. Thus, it could be possible to compare an untreated group in one cage with a treated group in another cage within the same farm at least a few days before and after the delousing occurred. However, different fish-groups within the same farm may come from different hatcheries or be of a different breed. In addition, there might be differences in environmental factors between cages within the same farm. Also, at some farms, there were few fish-groups left to compare with after exclusion. Another important unmeasured factor was the health status of the salmon prior to treatment. Diseases make the salmon more vulnerable to demanding procedures such as non-medicinal delousing operations. In Norway, there are several non-notifiable diseases important in regard to mortality, growth, and welfare of salmon, such as CMS, HSMI, and different bacterial diseases in addition to complex gill disease (Sommerset et al., 2023). Production data had inconsistent recordings of these diseases, making it difficult to adjust for effects caused by them.

We solved the problem of unmeasured confounding by finding the pre-treatment mortality and growth rate of each fish-group one week before treatment (unexposed) and subtracted this from the mortality and growth rate in a two-week period after treatment (exposed) to find the difference (treatment-associated mortality and growth) (Figure 12). The advantage of this approach is the possibility of adjusting the outcome for unmeasured variables. However, an apparent disadvantage is that we have no ‘true’ unexposed group. In addition, we risk adjusting for a negative effect associated with the last treatment when estimating the effect of the next treatment. This is the reason why we kept the risk period shorter than two weeks. This limited the studies to only looking at the short-term or direct effects of the treatment on mortality and growth, and not the long-term or indirect effects. The problem of adjusting effects related to prior treatments is reflected in paper II. The effect of reducing number of weeks between treatments on growth was significant, but the coefficient indicates that this had a positive effect on growth. This makes no biological sense, as the fish would have less time to recover. When changing the outcome to the growth rate five days before treatment, the analysis showed a significant negative effect. This indicated an additive negative effect on growth of treatments closer than two weeks.

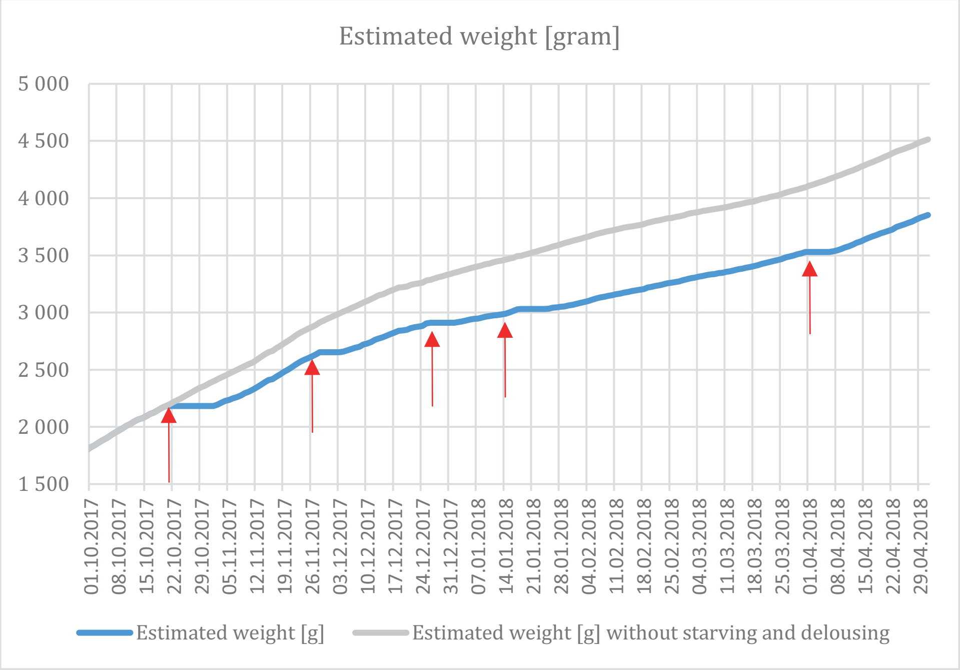

Figure 12. The graph shows an example of the growth of a fish-group within the dataset (blue line) being deloused five times (red arrows). The mean temperature in this example was 9.8^{0}C, and the mean TGC 2.64 from stocking to harvesting. The extrapolated growth (grey line) will follow the same growth rate as average TGC five days before treatment during the starvation period and one week after treatment. The grey line then resumes the same daily TGC as the treated group. It is assumed there is no compensatory growth, hence the distance between the grey and blue line will increase after each treatment.

When the study population is not randomly chosen, a selection bias is introduced (Dohoo et al., 2014a). An important selection bias in both studies I and II was not being able to trace all fish-groups throughout the entire production at sea. Even though we had the highest possible resolution of aquaculture data, 20.9% of the fish-groups were excluded in the growth study because they were impossible to trace. This highlights the importance of consistent tracing procedures to exploit industry data entirely in high-resolution analyses. Still, because many of these groups were split or merged with another group, one or several times during the production, this might also have biased the results if it had been possible to include them in the study.

Another obvious bias in this study was the inclusion of only three producers, all large companies. Only large companies were asked to provide data in order to increase the chance of achieving a satisfying spatio-temporal distribution of the different delousing treatments and simultaneously to reduce the time spent on data acquisition. In addition, companies normally use the same system for production data registration across different farms, which eases and reduces the possibility of introducing biases during data management. Even though this is a large dataset, it had an unequal spatio-temporal distribution. It has been shown that there is a significant variation in production loss (e.g., mortality and escapees) between companies in Norway, and on average the production losses are shown to be lower for larger companies and farms holding larger numbers of fish (Pincinato et al., 2021). This indicates that our results might not be transferrable to smaller companies (companies owning <20 farms). In addition, there is a spatial variation in the mortality pattern in Norway, where the mortality typically has been higher in the southern PAs (2-4), compared to the PAs in the middle (5-7) (Sommerset et al., 2022; Sommerset et al., 2023). The dataset thus covers some of this spatial variation, as the data covers 29.3% of all active farms in the study period, and 84% of the data coverage were in PAs 3-7. However, the environmental conditions and disease problems differ from the northernmost PAs (11-12) compared to the mid and south (Sommerset et al., 2023). These PAs are not represented, or are only in a minority, in the dataset. This means that it is difficult to extrapolate the results to other production areas or to small companies.

A bias possibly affecting mortality numbers would be the use of stun boats (Barrett et al., 2022). A stun boat is a harvesting vessel equipped with stunning, bleeding, and chilling systems. Barrett et al. (2022) found that stun boats often visited during treatment months, without any harvest being reported, indicating that these are used as standby in case of emergency harvest due to risky treatment operations. This means that mortality statistics might be underestimated, if fish are harvested because they are too vulnerable to be treated, or moribund after treatment (Barrett et al., 2022). The use of stun boats started around 2018, so this would only be a possible bias in the data from 2018 and 2019.

One of the main limitations in the growth study (paper II) is the fact that weight and growth rate of the salmon are estimated values in the production data. Even though keeping track of daily weight gain and growth rate of the farmed salmon is an important part of the production, it is time consuming to sample salmon from each cage to do weight and size measurements. In addition, it is also a question of how the sample represents the entire fish-group. In the production data, we had no means of knowing by which method the recorded weight of the fish was estimated, and if the method was equal across different companies, and even between farms within the same company. The daily weight gain in a cage will be estimated by the amount of feed given, number of fish, and the biological feed conversion ratio (bFCR). The bFCR is temperature and size dependent, and companies can use different models for estimating bFCR. It is necessary to know the bFCR to calculate the TGC. However, we did not know the bFCR since bFCR is an estimated value in the production data. Therefore, a simple approach was used where the same bFCR was assumed for all fish-groups during their entire production cycle. This approach did not adjust for the size dependency of bFCR and could cause a small underestimation of the treatment effect on growth. It is also possible that the feed amount did not perfectly reflect the appetite of the fish. However, this was largely accounted for by analysing the change in growth rate. In addition, since feed constitutes about 50% of the production cost (Iversen et al., 2020), the farmers have a strong incentive to reduce feed-spill.

5.2.8.2 Random error

Random error expresses the random variation inherent in the sampling process, and random error can be reduced by increasing sampling size (Dohoo, 2014). We would need 766 unexposed and 766 exposed cohorts to obtain a power of 80% and a confidence interval of 95%, assuming a weekly mortality risk of 1%, and a conservative estimate of the relative risk of three (Sergant, 2018). When accounting for a possible clustering, number of fish-groups per exposed/unexposed group would be 1 226, assuming an intracluster correlation (ICC) of 20% and four fish-groups within a farm (Dohoo et al., 2014e). In the mortality study, we ended up with 4 644 delousing treatments (fish-groups), and in the growth study 2 530 delousing treatments (fish-groups), which means we should have enough data to obtain a sufficient power for the study described in papers I and II.

Multilevel modelling reduces or removes the confounding due to unmeasured group-level confounders. In addition, it helps to quantify the random error correctly, because it improves the ability to obtain valid confidence intervals for estimates of effects at various levels of the hierarchy (Dohoo, 2014).

Even though the production data used for these studies contains the highest possible resolution, detailed descriptions of treatment-related information (such as use of well-boat or in-cage treatment, crowding procedures, temperature in treatment chamber and holding time), and information on disease status were inconsistent. Using production data for longitudinal cohort studies is data-demanding, partly because of the nature of clustering in salmonid aquaculture and also because the structure of the data for its intended use is not necessarily serving observational studies. Still, this high-resolution dataset made it possible to estimate the treatment effect on mortality and growth, and to use the distributions as input for the economic analysis.

5.2.8.3 Economic analysis

The validity of a partial budget analysis depends on the accuracy of the estimates and the assumptions made both in the economic model and in the modelled biological input variables in papers I and II.

There existed estimated values regarding the cost of some preventive methods (Holan et al., 2017), but we did not know how well these reflected the actual cost, and the estimations did not cover all the preventative methods. In addition, we did not have estimations regarding the cost of improvement of methods. Therefore, we chose not to include cost of prevention nor improvement. Thus, the partial budget model does not reflect the net benefit of preventing or improving, but rather how much a farmer could use before break-even. We also investigated how sensitive the model was to changes in key variables in a sensitivity analysis. Naturally, a partial budget model will not indicate whether one of the choices is the best alternative available, but only if one alternative is better than another alternative included in the analysis. In addition, it does not include evaluation of non-economic factors (less labour, safety issues, the benefit of alternating treatments, and environmental considerations). Another important issue with partial budget models relates to economies of size. It is reasonable to assume a linear relationship between input and cost-revenue for small changes, but a linear assumption might not hold if the changes become large. For example, in our analysis, labour is assumed to be a fixed cost, and not included in the analysis. However, if reducing number of delousing operations leads to heavily increased production, this could increase the need for labour.

The target population, the population to which it might be possible to extrapolate results from all three papers, is farmed Atlantic salmon in the on-growing phase at sea in Norway. The biological loss and possible economic gains of reducing this biological loss may not be transferrable to other countries, as they may have different ways of managing the problem of salmon lice, and other species within the Caligidae family of sea lice. In addition, the estimated biological losses might be higher for smaller companies.

5.3 Summary of papers

5.3.1 Estimating cage-level mortality distributions following different delousing treatments of Atlantic salmon (*Salmo salar*) in Norway

The objective of this study was to estimate the distribution of mortality after different delousing methods. We performed a retrospective descriptive study estimating cage-level mortality distributions after six immediate delousing methods: thermal, mechanical, hydrogen peroxide, medicinal, freshwater, and a combination of medicinal treatments. We investigated mortality patterns associated with 4 644 delousing treatments of 1 837 cohorts of farmed Atlantic salmon (*Salmo salar*) stocked at sea along the Norwegian coast from 2014 till 2017. The mortality was expressed as mortality rates. We estimated distributions of mortality rates within one, seven, and 14 days after all six delousing treatments, using mortality rate within seven days before treatments as baseline. The most important result from this study was a wide variability and positive skewness in mortality, showing a potential for improvement, especially for thermal treatments. The wide variability in delta mortality and variation between the treatment methods can be associated with the delousing method itself, the health condition of the fish, environmental factors, or managerial factors. We found that one can expect increased mortality after all six delousing methods. However, compared to the other delousing methods, the median mortality after thermal and mechanical delousing was the highest, about 5.4 (thermal) and 6.3 (mechanical) times higher than medicinal treatment, for the 2017 year-class. Further, the results suggest that the median mortality and variability in mortality for thermal delousing have been reduced from the 2014 to 2017 year-class, indicating an improvement in the technique. Still, a significant increase in the number of thermal treatments from 14 in 2015 to 738 in 2018 probably contributes to the overall increased mortality in Norwegian salmon farming.

5.3.2 How delousing affects the short-term growth of Atlantic salmon (*Salmo salar*)

The objective of this study was to investigate the immediate effect of delousing operations on the post-treatment growth of Atlantic salmon. To achieve this, we performed a retrospective cohort study using daily production data at cage-level from 2014-2019 from three large Norwegian aquaculture companies. We applied the registered feed-amount, number of fish, and seawater temperature at cage level to calculate differences in the thermal growth coefficient (TGC) of 635 fish-groups the week before the pre-treatment starvation period, to the week after 2 530 individual treatments. We categorised the different delousing operations into thermal, mechanical, hydrogen peroxide bath, freshwater bath, and combination medicinal baths. We modelled the effect on growth using a mixed effect linear regression model, with treatment method as the main fixed effect of interest, and included fish weight, seawater temperature, smolt-age, and year-class as fixed effects. In this study, we were able to quantify the growth loss and variation in growth loss after different delousing treatments. The period of starvation pre-treatment was followed by a period of suboptimal feeding and growth after all treatment methods, where non-medicinal treatment methods had a significantly larger negative effect on growth compared to medicinal treatments. Although the pre-treatment starvation period led to the largest share of growth loss (~75%) related to a delousing treatment, this shows that it is important to also include the potential growth loss after treatment (~25%) when calculating the total growth loss associated with delousing treatments. The results also suggest that the outcome of a treatment might be influenced primarily by factors such as treatment- related handling procedures, environmental conditions, or disease status of the fish-group. In an average cage of 150 000 salmon weighing 3 kg being treated at a seawater temperature of 10^0C, the short-term biomass-loss of one non-medicinal treatment was estimated to be 31 200 kg compared to not being treated at all. Thus, a potential exists for increased production in the Atlantic salmon aquaculture industry if it is possible to reduce the number of delousing operations.

5.3.3 The economics of preventing, replacing, or improving methods for delousing farmed Atlantic salmon in Norway

The objective of this study was to assess the economic consequence for a farmer of preventing, replacing, or improving current methods for delousing Atlantic salmon in Norway. To achieve this, we built a biological model simulating one production cycle of two different smolt-groups. We incorporated the risk of the biological losses (increased mortality and decreased growth) associated with different delousing treatments using Monte Carlo simulation. The outputs (harvested biomass, average end weight of the salmon, number of dead fish, and feed consumption) of production cycles without or with two, three, or four delousing treatments were applied as inputs in a partial budgeting model to assess the economic net benefit of different delousing regimes.

The results showed that sales value and feed consumption constitute the largest share of the change in profit between different treatment regimes. The biological cost of increased mortality and decreased growth associated with especially non-medicinal treatments is expected to be high, but varies substantially. The calculations implied that salmon producers could invest a considerable amount in measures for prevention or improvement of thermal treatments before break-even. For example, a farmer could spend on average 5.4 million NOK (535 313 €) per cage per 1-yearling production cycle on measures to prevent four thermal treatments before it was no longer economically beneficial. Depending on the performance of the four thermal treatments, 3.2 to 7.4 million NOK (319 196 -737 934 €) per cage per 1-yearling production cycle could be spent on measures of improvement. In other words, there exists a potential considerable economic incentive to prevent or improve the current non-medicinal treatment methods by ensuring good animal health and welfare. Replacing one thermal treatment with another immediate treatment method had a minor monetary benefit. Importantly, the results also showed that it is possible to improve factors leading to poorly executed thermal treatment methods because the distributions were truncated at the absolute minimum and maximum values recorded in the production data. It is important to account for the biological losses associated with lice treatments when making choices of delousing strategies. In addition, identifying risk factors related to non-medicinal treatments should be prioritised.

5.4 Discussion of main results

5.4.1 Biological losses associated with delousing operations

The results in papers I and II highlight the considerable negative effect that non-medicinal treatments have on farmed salmon health and welfare, and the fact that this effect varies substantially between treatments.

Before the large-scale implementation of non-medicinal treatments, strikingly little documentation existed on the effect of these methods on salmon health and welfare (Holan et al., 2017). Basic knowledge of upper temperatures and holding time for thermally treating salmon was lacking (Gismervik et al., 2019; Holan et al., 2017). Salmon cannot acclimate to temperatures above ~28 ^{0}C (Elliott & Elliott, 2010), and the seawater temperature in the treatment chamber was reported to be on average 31-34^{0}C (Hjeltnes et al., 2018; Hjeltnes et al., 2019). The temperature difference that salmon experienced between seawater in the cage and in the treatment chamber was approximately 22-22.5^{0}C (Hjeltnes et al., 2018; Hjeltnes et al., 2019). About three years after the large-scale implementation of thermal treatment, results from laboratory trials showed that fish exposed to high water temperatures (34-38^{0}C) for 72-140 seconds had instant behavioural responses indicative of pain (Nilsson et al., 2019) and acute tissue injuries in gills, eyes, brain, and possible also nasal cavity and thymus (Gismervik et al., 2019). By late summer 2019, the Norwegian government notified the aquaculture industry that thermal treatments could be forbidden in 2021, due to the issues of poor fish health and welfare (Riise, 2019). However, farmers had few alternative methods to turn to. And, as shown in papers I and II, the associated mortality and growth loss after mechanical treatments were not significantly different from thermal treatments. Thus, measures needed to be done to improve and document experience with the non-medicinal treatment methods.

The results in papers I and II show large variation in mortality and growth both within and between the different types of treatments. The variability is especially large between thermal treatments. Variation indicates an opportunity for improvement, if risk factors for increased mortality and reduced growth can be identified. One explanation for the large variation could be differences in treatment and handling procedures. In paper II, results show that the largest part of the unexplained variation in the outcome of treatments lies between and within subsequent treatments of fish-groups within the same farm within the same production cycle, adjusted for treatment method, year-class, smolt type, size of the fish, and seawater temperature. This suggests that the outcome of, for instance, a thermal treatment might be influenced primarily by factors such as managerial practices, environmental conditions, or disease status of the fish-groups. Treatment procedures include length of treatment time, temperature in treatment chamber, water pressure, etc. Handling procedures include length of crowding time, crowding density, pumping equipment etc. Handling, such as crowding and pumping, is an inherent part of most delousing operations and can cause stress, mechanical injuries, and mortality (Ashley, 2007; Delfosse et al., 2021; Erikson et al., 2016; Skjervold et al., 2001). Poor water quality in the well boat or treatment chamber is also a factor contributing to additional stress to the fish (Powell et al., 2015). Both thermal and mechanical treatments require the fish to be handled by crowding and pumping, and these handling procedures can vary. In our data, it was not possible to investigate the effect of treatment and handling procedures, as recording of this information was inconsistent. Longer treatment time and use of sedatives when thermally treating is shown to be associated with lower post-treatment mortality (Folkedal et al., 2021; Lund et al., 2022). In the study by Lund et al. (2022) it was suspected that crowding procedures also had an effect on mortality. However, like in our data, inconsistent reporting of crowding procedures made it difficult to investigate this effect.

The results from papers I and II indicate a possible improvement of the thermal treatments in the years after it was introduced. The median mortality declined from 2014 until 2019, and this trend appears to have been sustained into 2021 (Lund et al., 2022). In 2021, the government notified that thermal treatment would remain an option, if the effect on lice was good, and it was documented that the treatment was carried out in a way that secured good fish health and welfare (Norwegian Food Safety Authority, 2021). To help evaluate and document welfare, a welfare indicator scoring system was published in 2018 (Noble et al., 2018).

However, what the acceptable limit for poor fish health and welfare is, remains uncertain. Despite the decreasing trend in median mortality over the years, results from paper I show the median mortality after thermal treatments is 5.4 times higher compared to medicinal treatments for the 2017 year-class. And, despite increased focus on improving non-medicinal treatment methods in the past years, mechanical injuries after non-medicinal treatments are reported as the main reason for poor fish health and welfare in the on-growing period at sea in 2022 (Sommerset et al., 2023). Even though non-medicinal treatments most likely have improved, there is still a potential for further improvement of thermal and mechanical treatments and their use. In future studies investigating risk factors involved in delousing operations, estimating the effects of different handling and treatment procedures on mortality and growth should be emphasised. If detailed recordings of handling and treatment are made during a treatment, and are registered consistently across farms or even companies, and if it is possible to track fish-groups from stocking to harvest, a great potential lies in using production data for risk factor analysis.

In addition, measures probably need to be taken to reduce the number of times the salmon are deloused during the on-growing period, as the overall number of non-medicinal treatments peaked in 2022 (Sommerset et al., 2023). In our data, the salmon were normally treated four times, but this varied substantially and some groups were treated as much as eleven times. The additional effect of increased number of treatments and decreased time between the treatments during a production cycle, in addition to the effect of different diseases, gives the salmon little time and possibility for restitution. Even though salmon have a remarkable ability to compensate a weight loss, they do need some time for this (Hvas et al., 2022). Based on the results in papers I and II, and the study from Hvas et al. (2022), on average it does not appear that the salmon have sufficient time to compensate for the weight loss between the treatments, nor from the last treatment until harvest.

An important caveat of both studies described in papers I and II is that we were only able to analyse the short-term or direct effect of treatment on mortality and growth. We were not able to capture a possible indirect effect of treatment. Treatments and the treatment-related handling may have an indirect effect on mortality mediated by increased stress, scale loss, or injuries, making the fish more susceptible to diseases or secondary infections. For example, results from Riborg et al. (2022) suggest that shedding of the bacteria *Yersinia ruckeri*, which causes haemorrhagic septicaemia, is provoked by handling and thermal treatment. Since we were not able to measure such indirect effects, we could not estimate the total effect of delousing on mortality and end harvest weight. Further studies are needed to investigate the total effect of delousing treatments on mortality and growth, and the extent of compensatory growth.

The purpose of a delousing treatment is obviously to remove lice so the infestation pressure and damage caused by lice on both farmed and wild salmon is reduced. It is a paradox that the most applied treatment methods and the related handling are themselves harmful to the farmed salmon. Results from papers I and II show that this leads to huge biological losses.

5.4.2 The economic impact of delousing operations

The discipline of economy deals in general with how to allocate resources when they are scarce, so as to aid a decision on whether to choose one alternative over several others. When making a choice, there must be some sacrifice, and this sacrifice generates a cost called the opportunity cost (Rushton, 2009b).

The simplest form of an economic evaluation is a cost estimation, such as the cost of a disease or a programme, without comparison of alternative options or the cost of the outcome (Rabarison et al., 2015). Measuring the monetary cost of a disease is important when assessing the relative importance of different diseases, as in the global burden of animal diseases (GBAD) initiative for animals (Rushton et al., 2018). Simple cost calculations can aid prioritising which diseases need to be dealt with first. One of the costliest obstacles faced by the Norwegian salmonid aquaculture is described to be the challenge with salmon lice (Abolofia et al., 2017; Iversen et al., 2020; Iversen et al., 2017). However, we don't have a good overview of how much other diseases in Norwegian aquaculture may cost. An important reason for this is an insufficient overview of the prevalence of diseases regarded as important contributors to mortality and poor fish health and welfare. This is because many of these diseases are non-notifiable. In addition, there is no harmonised way of categorising mortality causes. However, work on implementing a standardised way of categorising mortality causes is on-going (Aunsmo et al., 2023). This will be of great help to model the economic burden of different diseases in Norwegian salmonid production thus will aid prioritising which diseases need to be dealt with first and to prioritise interventions. In addition, surveillance and reporting of several of the non-notifiable diseases in Norway (Dyrehelseforskriften, 2022) would give a better overview of their prevalence.

Simply calculating the cost of an intervention will be of limited use when choosing between interventions. To make an economically rational choice, the decision needs to generate the greatest benefit relative to the cost (Rushton, 2009b). The cost and benefit ratio of different alternatives may not be obvious. For example, as shown in paper III, medicinal treatments are cheaper compared to non-medicinal treatments because they have a significantly lower associated biological loss. However, if the biological loss was not included, they would cost more (0.36 NOK/0.036 € per kg treated) compared to thermal (0.32 NOK/0.032 € per kg treated) and mechanical (0.29 NOK/ 0.029€ per kg treated) treatment. In addition, medicinal treatments have a restricted use because of the issue of resistance. If the cheapest option is less effective or has serious side-effects, such as increased risk of death or growth loss, the decision of which intervention to choose might be unclear. Comparing alternative costs and benefits can help to decide which intervention is the best alternative, or how much money is economically justifiable to use on one alternative compared to another.

Since the aim of our last study (paper III) was to assess the economic consequences of different delousing regimes, a partial budgeting model was chosen. The primary goal of the bio-economic model was to highlight the cost of the biological loss associated with different treatment methods, and show how much money could be used on preventive measures in addition to measures of improvement before it is no longer economically justifiable.

The production cost incurred is an important element in a partial budgeting model. Here, only the costs that vary if choosing one delousing method over another shall be included (Rushton, 2009a). For instance, in our model, the choice of delousing method does not affect number of smolts stocked in a cage and the buying price of a smolt. The smolt cost is therefore irrelevant. Feed cost however, is relevant. Feed cost will vary between different delousing methods in regard to how many salmon die and when they die, and how many survive and need to be fed. In addition, if one delousing alternative results in lower mortality and growth loss over another, this yields added return due to more saleable biomass.

The results in paper III most importantly suggest that accounting for the biological losses associated with lice treatments is important when choosing delousing strategies. The biological costs of increased mortality and decreased growth associated with especially non-medicinal treatments are expected to be high, even though they vary substantially. Salmon producers can invest a considerable amount in measures for prevention or improvement of non-medicinal treatments, depending on the number and performance of the treatment, before break-even. For instance, a farmer can use almost 7.5 million NOK (742 280 €) per cage more on measures to prevent four poor performing thermal treatments (9.64 million NOK/954 077 € per cage), compared to what he can use on four good performing treatments (2.18 million NOK/215 756 € per cage), for a 1-yearling. Poor and good performing would be equal to the 5% worst and best performing treatments described in paper III. However, the current amount a farmer can spend on measures to prevent or improve might be smaller than stated here, as the technical solutions in aquaculture of Atlantic salmon in Norway progress quickly, and the dataset underpinning the calculations ends in 2019.

5.4.3 How can bio-economic modelling support decision-making?

The bio-economic model described in paper III is limited by how much and what type of information is put into the model. As Box et al. (2009) state: 'All models are wrong, but some are useful'. Hence, an important question is for what particular purpose the economic model is useful. This bio-economic model is a useful tool to help strategic production planning in the long run. For example, if a company is planning a new production with a certain delousing treatment regime, the model can answer how much effort could be made in improvements or replacements in treatment methods and use. It can also support policy makers looking into incentives for farmers to improve, prevent, or replace their methods. On the other side, the model is of limited support to a farmer's daily or short-run decisions. For example, a farmer might be interested in questions such as: 'If treating a cage with fish weighing on average 4 kg with suspected CMS, and the water temperature is 10^0C, what would be the expected outcome of a thermal treatment compared to a mechanical treatment?' The bio-economic model cannot answer such fine-grained questions. To do this, additional data is needed regarding disease status of the fish, crowding procedures, pumping and treatment time, and additional epidemiological studies looking into the effect of each step of the treatment. In addition, a farmer often has limited choices. Even though the model shows that thermal treatment should be avoided or replaced, this will not be possible if thermal treatment is the only available option at the moment.

Controlling disease is a crucial part of animal production. Without models suitable to support decisions of if and how to treat against salmon lice, it is understandable that farmers might rely on intuition and experience in their decision process. As Osmundsen et al. (2017) describe: 'We see that the fish farmers describe a decision making context fraught with uncertainty and uncontrollable externalities'. And cited by a farmer: 'My decision support tool is experience, and that is the most important one' (Osmundsen et al., 2017). However, although experience and intuition can be useful tools, it is proven that the mental short cuts (heuristics) most human employ when making judgements under uncertainty could lead to systematic and predictable errors (Tversky & Kahneman, 1974). It is apparent that no model can, nor should, implement the whole complexity of the production of Atlantic salmon with all its risks and uncertainties. However, setting up a model, such as a partial budget, can help to prevent both systematic and predictable errors by structuring information and highlighting potential prospective costs that may be avoided if action is taken. The biological loss associated with treatments against salmon lice is such a future cost; a cost that will keep on running until measures are made to reduce it.

Several mathematical models are available to guide management decisions and to understand complex interactions between sea lice, their wild and farmed hosts, and the environment (Groner et al., 2016). However, there is also a need for both simple and more complex bio-economic models that incorporate risk and uncertainty by the use of production data and epidemiological research to aid well-founded decisions. The bio-economic model described in paper III highlights the importance of incorporating the risk of increased mortality and reduced growth associated with different treatments because, when doing so, it also highlights the economic incentive for improving methods to ensure good health and welfare for the salmon.

5.4.4 What is a sustainable management of the salmon lice challenge in aquaculture?

Sustainability is defined as 'meeting the needs of the present without compromising the ability of future generations to meet their own needs' (Bruntland, 1987). The impacts of salmon lice is a major challenge for sustainable production of farmed Atlantic salmon in Norway, and has become the most important obstacle to the stated political goal of quintupling aquaculture production by 2050 (Vollset et al., 2018). Substantial treatment-associated mortality and growth loss is a challenge in regard to reduced fish health and welfare, and an inefficient use of resources.

Sustainable management of the salmon lice challenge is thus a vital part of a sustainable aquaculture industry.

Sustainable management of the salmon lice challenge is closely linked to the concept of integrated pest management (IPM), a concept strongly influenced by the growth of and progress in agriculture. The US Statewide IPM program defines IPM as:

> An ecosystem-based strategy that focuses on long-term prevention of pests or their damage through a combination of techniques such as biological control, habitat manipulation, modification of cultural practices, and use of resistant varieties. Pesticides are used only after monitoring indicates they are needed according to established guidelines, and treatments are made with the goal of removing only the target organism. Pest control materials are selected and applied in a manner that minimizes risks to human health, beneficial and nontarget organisms, and the environment. (University of California Agriculture & Natural Resources, 2023).

The main aim of pest management is not to eliminate a pest organism, but to bring it into acceptable bounds (Norris et al., 2003). A fundamental part of an IPM is thus farming practices that are compatible with ecological systems such that organisms are not elevated to pest status, while keeping the use of pesticides and other interventions to levels that minimise risk to humans and the environment (Lewis et al., 1997). It also encourages the use of biological control mechanisms by natural enemies. IPM therefore takes an ecosystem approach (Norris et al., 2003), and is a critical part of a sustainable aquaculture-ecological system.

In the light of the definition of integrated (sustainable) pest management, it can be argued that the past 40 years of managing salmon lice has not succeeded in ensuring sustainable pest management. The salmon farming production has not been designed to naturally limit the elevation of the salmon lice to a pest status, as a large part of the production mainly occurs in open sea cages. This has led to several negative environmental externalities, such as increased infestation pressure on the wild salmonid population, negative effects of medicinal spillover to non-target organisms, and negative effect on native populations of wrasse and lumpfish.

The central management strategy of salmon lice has suffered from the same key weakness as agriculture has, which is reliance on therapeutic tools as primary means of controlling, rather than using them occasionally (Lewis et al., 1997). Using therapeutic tools as primary means of control might have been economically sound in the short run by allowing an ongoing increase in production, but in the long run it has led to problems with resistance and negative externalities. In addition, the producers have not taken a sufficiently active approach to understanding natural enemies and how they function as a part of the ecosystem. This is exemplified in the use of cleaner fish as a biological pest control and the way they have been applied in large numbers at a relatively low cost, with little emphasis on their biology and how to promote their natural effectiveness (Barrett et al., 2020b; Overton et al., 2020). This has led to an unacceptable high mortality and poor health and welfare of cleaner fish (Sommerset et al., 2023). Further, the technological race towards non-medicinal treatment methods did not give sufficient consideration to the biology of the farmed salmon, leading to high mortality and growth loss. Paper III shows that this has been, and is, causing high economic losses to the farmers. The farmers experienced the difficult situation of keeping below the legal limit of lice when few treatment options exist, and at the same time maintaining large-scale production of salmon around 2015. This might explain why insufficient consideration was given to the health and welfare of the farmed salmon, in the large-scale implementation of the non-medicinal treatment methods. Obviously, there is no silver bullet when tackling the salmon lice challenge. Ongoing work is promising, as demonstrated by two examples: the technology of submerged, semi-closed, and closed cages to create a barrier between the salmon and the lice (Barrett et al., 2020a; Sievers et al., 2022); and mixing different preventive measures (Oldham et al., 2023).

To ensure sustainable growth of the salmon industry in Norway, the traffic light system was implemented in 2017 (Vollset et al., 2018). Currently, the only sustainability indicator used to ensure sustainable growth of the salmon industry is the effect that salmon farming spillover of salmon lice has on wild salmon mortality. The measurement of this effect became heavily debated, and in a paper trying to disentangle the role of salmon lice on the marine survival of Atlantic salmon, the authors write: ‘Using a single model and parameter to determine management advice is not warranted, as no single data point reflects the natural complexity of nature’ (Vollset et al., 2018).

Sustainable management of salmon lice needs to weight several different aspects such as mortality on wild salmon stock, other environmental impacts, farmed salmon and cleaner fish health and welfare, and production economy. Discussion is currently ongoing about using farmed salmon mortality as an additional sustainability indicator (Menon Economics, 2022). The large variation in mortality between farms within a region (Bang Jensen et al., 2020; Menon Economics, 2022) indicates that it would probably be more efficient to implement mortality as a sustainability indicator at farm-level rather than at region level (Menon Economics, 2022).

The mortality in the on-growing phase is still too high, and what we might also need is an increased focus on the value of farmed salmon. Even though the results from the economic model in paper III shows that there possibly exists great economic benefit from ensuring good animal health, it does not show that the value of the fish should exceed its selling price. The production systems and their associated value chains have become very efficient and livestock has been reduced in value relative to other goods in society (Rushton, 2017). Further, the separation between people and livestock through the process of urbanisation, where animals are raised, slaughtered and processed out of sight of urbanised people, leads to a depersonalisation of the animals (Rushton, 2017). This depersonalisation becomes a problem because the consumers will dictate the value (e.g., selling price) of the farmed animals, and by that the means in which they are kept (Rushton, 2017). The difference between economic and animal health approaches leads to frustration because these two disciplines have different approaches to evaluating animal health and welfare (Rushton, 2017). The frustration lies in the value of welfare and good health of livestock animals being reduced to the selling price. Farmed fish also have an intrinsic value. Defining intrinsic value is a difficult task because it is a multifaceted concept that can be considered from various angles of philosophical inquiry (Batavia & Nelson, 2017). However, it could be defined as the value a thing has for itself in contrast to the value it has for something or someone else (instrumental value) (Batavia & Nelson, 2017). Importantly, though intrinsic value is attributed by humans, it does not need to be attributed only to humans (Batavia & Nelson, 2017).

It is obviously not an easy task to include an intrinsic value in addition to an instrumental value in decision making. Still, even though a difficult task, we should not ignore it. As Batavia and Nelson (2017) suggest '… nonhuman intrinsic value and the obligations it entails ought to be treated seriously, as moral propositions, in conservation planning and decision-making'. Thus, in addition to the economic incentive of securing good animal health and welfare, we also have a fundamental moral responsibility (Dyrevelferdsloven, 2010).

So, referring to the title of this thesis, *What is the value of a dead fish*? the answer is, basically nothing. However, this work shows that this is not the question we should be asking. It is the opposite, namely: what is the value of a fish that is alive and thriving? Because here lies the great potential in not only increasing production and profit, but also ensuring a sustainable and ethically sound production.

5.5 Conclusions

The overall aim of the thesis was to assess the biological and economic impact of delousing farmed Atlantic salmon in Norway, focusing on non-medicinal treatments. We have shown that increased mortality and decreased growth of farmed salmon is associated with these treatments, and this constitutes a cost to the farmer that is expected to be high, but varies substantially. Therefore, the economic benefit of preventing or improving especially non-medicinal treatments can also be high.

With respect to salmon lice management, salmon producers in Norway can benefit from optimising the resources used for non-medicinal treatments. The model presented in this thesis documents how it is possible to invest a considerable amount in measures for prevention or improvement of non-medicinal treatments before break-even. The increased economic output achieved from reduced mortality and higher growth rates also comes with a potentially large improvement in fish health and welfare.

The work in this PhD shows that knowledge of both the effect from treatment measures and their side effects are important when deciding on treatment strategies, and accounting for the biological losses associated with lice treatments is essential when making choices of delousing strategies. In the years to come, emphasis should be placed on following the principles of integrated pest management to ensure a sustainable management of salmon lice. This should be done through interdisciplinary research and by comparing all the different aspects of the impact of salmon lice against each other.

5.6 Future perspectives

"You know," said Arthur, "it's times like this, when I'm trapped in a Vogon airlock with a man from Betelgeuse, and about to die of asphyxiation in deep space that I really wish I'd listened to what my mother told me when I was young." "Why, what did she tell you?" "I don't know. I didn't listen."

-Douglas Adams, *The Hitchhiker's Guide to the Galaxy*, 1979

Further work on finding the risk factors for mortality and decreased growth after thermal and mechanical treatments should remain a high priority. In addition, other negative side-effects of managing the salmon lice challenge should not be forgotten, such as the negative effect on cleaner fish health and welfare. Future work also needs to be done in regard to the long-term effect of non-medicinal treatments on mortality and growth loss. In addition, the possible effects of delousing methods on the slaughter quality of the salmon should be investigated.

Great advantages and possibilities lie in using production data for observational studies, especially if additional information related to managerial practises, treatment procedures, and mortality causes is registered, and, importantly, if the production data enables tracking of fish-groups from stocking to harvest. Even though the salmon lice challenge is one of the costliest challenges in Norwegian salmon aquaculture, we don't have a good overview of what other diseases may cost, especially the non-notifiable. Continuing the ongoing work related to standardisation of mortality causes and implementing surveillance and reporting of several of the current non-notifiable diseases (Dyrehelseforskriften, 2022) would be a great contribution to calculating the economic burden of different diseases in Norwegian salmonid production, and prioritising interventions.

Societal costs, such as negative externalities, have not been covered here. The previously applied medicinal treatment spillover to the environment had negative effects on environment, which was not reflected in the production cost of farmed salmon, thus being a negative externality to society. With the shift from medicinal to non-medicinal treatments, the negative environmental effects on non-target organisms are reduced. However, as is evident from studies I and II, the non-medicinal treatment significantly affects the farmed salmon health negatively compared to medicinal treatments, which leads to economic losses to the industry. These negative effects of the non-medicinal treatments are as such not defined as externalities as they are internalised by the companies in the biological loss. It could be interesting to investigate if the biological loss associated with delousing treatments manifests in higher salmon prices due to increased production costs, decreased supply, and a high demand, or if the biological loss actually reduces the salmon producing companies' profitability. In other words, who takes the greater share of the cost of the biological losses: the companies or the consumers?

Creating new methods for combating the lice requires investments. Recently, many investments made in the Norwegian salmon farming industry have been put on hold due to the implementation of a new ground rent tax (Stranden, 2022). It will be interesting to see if this affects the investments done to improve or prevent delousing treatments in the future.

In regard to governing the commons (ensuring sustainable aquaculture and management of the salmon lice challenge) it could be interesting to look into work related to analysing social-ecological systems (Ostrom, 1990). It might be, that one size fits all across the different levels (i.e., production areas, companies) is not the soundest solution.

And last, but not least, epidemiological and economic modelling are tools to use in an overall decision-making process. Fundamental to this is also consciousness of our moral responsibility. I believe that we also need to grasp the fact that nature has a value beyond serving as an 'ecosystem service' to us humans. If we don't manage to grasp this, we are in great trouble when deciding how the future should look and if it should be sustainable or not.

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7 Papers I-III

Paper I

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RESEARCH ARTICLE

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Estimating cage-level mortality distributions following different delousing treatments of Atlantic salmon (*salmo salar*) in Norway

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Abstract

This retrospective descriptive study estimates cage-level mortality distributions after six immediate delousing methods: thermal, mechanical, hydrogen peroxide, medicinal, freshwater and combination of medicinal treatments. We investigated mortality patterns associated with 4 644 delousing treatment of 1 837 cohorts of farmed Atlantic salmon (*Salmo salar*) stocked in sea along the Norwegian coast between 2014 and 2017. The mortality is expressed as mortality rates. We found distributions of delta mortality rate within 1, 7 and 14 days after all six delousing treatments, using mortality rate within 7 days before treatments as baseline. The results show that we can expect increased mortality rates after all six delousing methods. The median delta mortality rates after thermal and mechanical delousing are 5.4 and 6.3 times higher than medicinal treatment, respectively, for the 2017 year-class. There is a reduction in the delta median mortality for thermal and freshwater delousing from 2015 to 2019. There is a wide variability in the mortality rates, in particular for thermal delousing. Our results suggest that the variability in delta mortality for thermal delousing has been reduced from the 2014 to 2017 year-class, indicating an improvement of the technique. However, a significant increase in the number of thermal treatments from 14 in 2015 to 738 in 2018 probably contributes to the overall increased mortality in Norwegian salmon farming.

KEYWORDS
aquaculture, Atlantic salmon, delousing, mortality, salmon lice

1 | INTRODUCTION

There is a growing concern regarding increasing mortality of farmed Atlantic salmon (*Salmo salar*) in Norway (Bang Jensen et al., 2020; Tørud et al., 2019). In the seawater phase of the production, the total cumulated mortality of salmonid fish increased from 2014 to 2018, from 14.3% to 16.8% of the standing stock (Bang Jensen, Qviller, et al., 2020). The increasing mortality constitutes a serious welfare problem as well as an economic challenge. Treatment against salmon lice by physical removal of the lice (so called non-medicinal treatments) has been discussed as one of the reasons for the increased mortality in the seawater phase of the production (Bang Jensen, Qviller, et al., 2020; Hjeltnes et al., 2019; Oliveira et al., 2021; Overton, Dempster, et al., 2018).

Salmonid aquaculture has struggled with salmon lice since its inception (Costello, 2009). The extensive use of lice treatments has a severe financial impact. The total cost of controlling salmon lice in Norway was estimated at 8.70% of the Norwegian industry`s total value in 2011 (Abolofia et al., 2017), and NOK 5 billion per year in 2017 (Iversen et al., 2017).

Salmon lice *Lepeophtheirus salmonis* (Krøyer, 1837) are naturally occurring ectoparasites that can infest salmonid fish in salt water in the Northern hemisphere (Pike & Wadsworth, 1999). The parasite feeds on the mucus, skin and blood of the host, causing mechanical damage and osmotic stress. If the infection levels increase beyond the hosts ability to compensate, salmon lice can cause pathology and even be lethal to its host (Finstad et al., 2000; Pike & Wadsworth, 1999). However, in Norway the maximum permitted number of adult female lice per cultured fish ensures that pathology in the fish rarely occurs (NFD, 2012). To keep lice levels below the legal limit, farmers use different preventive measures as for example, cleaner fish or so called “lice skirts”, but they are still dependent on measures for immediate delousing.

Over a long time period, large-scale reliance on a few chemotherapeutants to control salmon lice has resulted in a drift towards resistance (Denholm et al., 2002; Myhre Jensen et al., 2020). Today, salmon lice display reduced sensitivity and/or resistance towards all available chemotherapeutants, except benzoylphenyl ureas (Aaen et al., 2015; Helgesen et al., 2020). Around 2015, thermal and mechanical delousing methods were introduced as non-medicinal substitutes (Helgesen et al., 2020; Overton, Dempster, et al., 2018), and from 2015 to 2016, the industry rapidly shifted from medicinal to non-medicinal treatments. Currently, in Norway thermal and mechanical delousing are the most frequently applied treatment methods for immediate removal of salmon lice (Helgesen et al., 2020). In 2019, about 3.3 non-medicinal treatments occurred for each medicinal treatment event (Myhre Jensen et al., 2020), and of all immediate delousing treatments performed in 2019, 54% were thermal and 27% mechanical (Oliveira et al., 2021).

Previous studies and reports from field indicate both injuries and increased mortality after mechanical, thermal and hydrogen peroxide treatment (Hjeltnes et al., 2018; Overton, Dempster, et al., 2018; Overton, Samsing, et al., 2018). Less is known about mortality after freshwater treatment. Most of the immediate delousing methods involve crowding and pumping, which is stressful for the fish (Ashley, 2007). The principle of thermal treatment is to inactivate the lice by exposing salmon and lice to warm water for a short time (Grøntvedt et al., 2015; Roth, 2016). In mechanical delousing, the lice are removed by either brushing or flushing the louse from the fish (Gismervik et al., 2017; Nilsen et al., 2010). Exposing Atlantic salmon to warm water can lead to aversive reaction and injuries (Gismervik et al., 2019; Moltumyr et al., 2021; Nilsson et al., 2019).

Salmon mortality is a negative effect of delousing. To our knowledge, mortality after different delousing methods has not been quantified and compared on a cage level. Neither has the change over the past years been explored. There can be large variation in mortality between groups of fish within a site (Bang Jensen, Qviller, et al., 2020). Production data from aquaculture companies have a cage-level resolution, which makes it possible to describe variation between groups of fish when looking at mortality after delousing. If variability in mortality after delousing exists, a potential for reducing the mortality also exists. Knowledge of both the effect from treatment measures and their side effects in terms of biological and financial losses is important when deciding on treatment strategies. Therefore, the aim of this study is to estimate the mortality distribution after different delousing treatments on a cage level to aid understanding the potential for reducing biological losses and provide a fundament for an up-to date cost estimation for salmon lice treatments.

2 | MATERIALS AND METHODS

2.1 | Study population

Salmonid farming commonly consists of a freshwater and a marine phase. Stocking of smolt in marine farms occurs in either the spring or the fall, and fish are kept in cages until slaughter, usually after 14–19 months. Fish stocked in the same year is here defined as a year-class. A marine farm is usually comprised of several cages, with a legal maximum limit of 200 000 fish per cage (NFD, 2008b). During the marine phase, groups of fish are often moved, and sometimes split or merged between cages within a farm. On occasion, they are also transferred between farms.

Five large Norwegian salmonid farming companies (companies with over > 20 farms operating in multiple production zones) were asked to provide data for this study. Three companies agreed. We choose to ask only large companies to provide data for this study to increase the chance of achieving a satisfying spatio-temporal distribution of the different delousing treatments.

We received data describing four year-classes of farmed Atlantic salmon stocked in sea at 295 farms (210 unique) along the Norwegian coast, from 2014 to 2017. The study period started in year 2014 and ended in 2019. During the study period there were 717 active farms along the coast. Since 2017 the Norwegian coast has been divided into 13 production zones, based on hydrographic properties and estimated capacity of production (Ådlandsvik, 2015; NFD, 2017).

2.2 | Data

Norwegian aquaculture farming companies register daily production data concerning stocked fish, mortality numbers, treatments, feeding, lice counts, environmental data etc. (NFD, 2008a). The data consist of cage-level historical production data related to salmon lice treatments and mortality, registered from 2014 to 2019. Two of the companies extracted the data directly from their production data monitoring system. AquaCloud, a digital database standard for the aquaculture industry in Norway (NCE Seafood Innovation, 2017), provided data on behalf of the third company. One company delivered accumulated production data related to a salmon lice treatment on the following different time periods: within 7 days before treatment, on the treatment day, and within 7 and 14 days after treatment. The other two companies supplied daily production data. Since registration of production data in AquaCloud started first of January 2017, production data concerning the 2015 and 2016 year-class from one company were incomplete. However, the year-class of 2014 was complete as AquaCloud used this as an initial trial data set.

The data included the following variables: production zone, company name, year-class, farm identification number, cage identification number, fish group number, date of delousing, method of delousing, active substance (in case of medicinal treatment), number of fish, estimated average weight of fish, and number of dead fish.

A key in understanding the dynamics of mortality is the possibility to follow the same cohort before and after treatment. In this study, a cohort is a group of fish defined by production zone, company, farm number and cohort identification number. When cohorts are deloused, they are often transferred from one cage to another. In these cases, tracking groups of fish before and after treatment based on cage number is not possible. At stocking the different groups of fish are usually designated a number in the production data. In more recent production data, this number serves as a consistent identification number, making it possible to track the same cohort from stocking in sea to harvesting. In the accumulated data set provided by one company, all the cohorts had a consistent identification number 7 days before and 14 days after treatment, but only the year-class of 2016 and 2017 had an identification number consistent from stocking to harvesting. In the two data sets with daily registration, several cohorts did not hold a consistent identification number and the fish group number designated to the cohorts in the production data, changed when the group transferred from one cage to another, and split or merged with other cohorts. In such cases, the high resolution of the daily production data often made it possible to detect and trace cohorts by comparing estimated average weight and number of fish in each cage before and after transfer. We traced the cohorts 7 days before to 14 days after treatment, or if feasible from stocking to harvest, and gave them a unique identification number. After this process, about 20% of the original identification numbers from one daily data set, and 50% from the other daily data set, remained.

Occasionally, there were movements of several groups of fish with approximately equal weights and numbers to different cages at the same day, or adjustment of weight and number in a group during handling/transfer. As a result, the weight and number before and after movement between cages is not always identical. Therefore, we cannot dismiss the possibility that some cohorts were not correctly traced. These examples also highlight the importance of consistent tracing procedures to exploit industry data entirely in high-resolution analyses.

Production data concerning species other than Atlantic salmon were excluded from the study data. Moreover, farms that were registered at the Directorate of Fisheries as brood stock, hatcheries or research farms were also excluded. Further, cohorts were excluded if they were moved from one farm to another, split or merged with other cohorts, or impossible to trace. We categorized the cohorts in the following weight-classes: <2kg, 2-3kg, 3–4 kg, 4-5kg and > 5 kg in order to describe delta mortality over different weight-classes.

2.3 | Salmon lice treatments

The production data included information on the date of treatment, cause for treatment, treatment method and active substance. Based on this information delousing treatments were divided into six different categories as presented in Table 1. It was not possible to categorize delousing as treatment in cage or well boat, as recording of this information was not consistent. We did not expect that delousing with medicinal feed would give increased mortality (Veterinærkatalogen, 2020); therefore treatment with medicinal feed was not included in this study. Hydrogen peroxide and freshwater treatment against only amoebic gill disease (AGD) was excluded. Hydrogen peroxide and freshwater treatment against both AGD and salmon lice were included.

2.4 | Calculating mortality rate

Mortality during four different time periods: within 7 days before delousing and within 1, 7 and 14 days after delousing were set to ensure comparability of all the data included in the study and under the assumption that the effects of delousing would decrease after two weeks. Any extension after two weeks was not attempted, with the risk of accidently including any subsequent delousing. During the four different time periods of interest, fish could leave the cohort for other reasons than death, for instance slaughter or sampling. A cohort was included in the study even if the entire cohort were slaughtered between 8 and 14 days after treatment. Premature withdrawal or entering of animals during the time period defines a dynamic cohort; hence, the appropriate incident measure of deaths is mortality rate (Mrate) (Toft et al., 2004).

We calculated the mortality rate for the four different time periods using Equation 1 (Toft et al., 2004). The time periods are expressed in number of days. Thus, the denominator is an approximation of number of fish days at risk, and Mrate is expressed in number of dead fish per fish-day.

$$Mrate = \frac{number\ of\ dead\ fish\ during\ time\ period}{\frac{number\ of\ fish\ at\ risk\ at\ start + number\ of\ fish\ at\ risk\ at\ end}{2} x time\ period} \tag{1}$$

We set the mortality rate within 7 days before delousing as baseline mortality, and subtracted this from the mortality rate at 1, 7 and 14 days after delousing to find the change in mortality rate, referred to as delta mortality rate, ΔMrate (equation 2). The ΔMrate will have a positive sign in case of increased mortality after a delousing compared to the mortality prior to treatment, or negative in the opposite case.

$$\Delta Mrate = Mrate_{-post\ treatment} - Mrate_{-prior\ treatment} \tag{2}$$

2.5 | Data management and descriptive statistics

Data management and statistical descriptive analysis was performed in the statistical software package Stata ® SE 15.1 (StataCorp, College Station, Texas USA) and Microsoft ® Office Excel (bar diagrams). We produced tables, box plots and graphs with the calculated ΔMrate and its distribution over year, year-classes and weight-classes.

TABLE 1 Categories ($n = 6$) of delousing operations applied in farmed Atlantic salmon in three Norwegian companies from 2014–2019

Categories ($n = 6$) of delousing operations	Description of category of delousing operation
Thermal	Non-medicinal treatment using heated seawater. Includes all treatments using: a. Optilice® b. Thermolicer c. Heated seawater
Mechanical	Non-medicinal treatment using brushing or flushing. Includes all treatments using: a. FLS Avlusersystem b. Hydrolicer c. SkaMik d. Flushing or mechanical treatment
Hydrogen peroxide	Hydrogen peroxide (H2O2) bath in cage or well boat
Medicinal bath	Medicinal bath in cage or well boat using one of the following active substances: a. Azamethiphos b. Cypermethrin c. Deltamethrin d. Imidacloprid e. Other
Freshwater bath	Freshwater bath in cage or well boat
Combination	Treatment of the same cohort with two different delousing methods on the same day. Includes the following combinations: a. two different active substances b. hydrogen peroxide and medicinal bath

2.6 | Transformation of ΔMrate to number of dead fish

We used the distribution of ΔMrate obtained for each of the six different treatment categories, to find the median ΔMrate. We transformed the obtained median ΔMrate to number of dead fish to provide an example of the absolute median number of accumulated dead fish following the different delousing treatments. The accumulated number of dead fish 14 days after treatment, is calculated using Equations 3 and 4 (Toft et al., 2004). Nt is the number of fish in the end of the period (t), N0 is the number of fish at start set to 150 000 fish, e is Euler's number, Mrate is median ΔMrate 14 days after the six different treatment methods and t is time period which is 14 days. If ΔMrate is negative, this gives a negative number of accumulated number of dead, meaning fewer fish die after the treatment, than before.

$$N_t = N_0 e^{-Mratext} \tag{3}$$

$$N_0 - N_t = \# dead \tag{4}$$

3 | RESULTS

3.1 | Salmon lice treatments

The data set originally consisted of 6 131 delousing treatments of four year-classes of Atlantic salmon in 295 farms (210 unique) during 2014–2019. After exclusion of cohorts that were split or merged, or not possible to trace, the data set consisted of 4 644 delousing treatments (N) (Table 2) in 214 farms (159 unique) in 1 837 cohorts consisting of about 24.7 billion fish. The first delousing occurred in May 2014 and the last in April 2019.

TABLE 2 Overall frequency of treatments within the different categories from year 2014 to 2019. The treatment category “Combination” contains combination of two different medicinal baths or combinations of hydrogen peroxide bath and medicinal bath

Delousing category	Frequency	Per cent
Thermal	2 692	57.97
Mechanical	619	13.33
Hydrogen peroxide	445	9.58
Medicinal bath	198	4.26
Freshwater bath	172	3.70
Combination	518	11.15
Total	4 644	100

Table 2 shows the overall frequency distribution of treatments for the six delousing categories. More than half of the treatments are thermal delousing (58%), while the categories “medicinal baths” and “combination” constitutes 15%. Table 3 shows the frequency distributions of treatment categories from 2014 to 2019. Most treatments are performed in 2015–2018, since the data are gathered per year-class. From 2015 to 2016, there is a pronounced shift in the frequency distributions of treatments. In 2015, half of the total amount of treatments is combination, over 30% hydrogen peroxide baths and only 2,6% of the total amount of treatments is non-medicinal (thermal and mechanical). In 2016, the non-medicinal treatments make up 78% of the total amount of treatments, and 54% of the total amount constituted of thermal treatments. There is also an increased use of freshwater baths, and at the same time a decrease in hydrogen peroxide baths and combination treatments. The main share of treatments continues to be non-medicinal treatments from 2017 to 2019. Table 4 shows the frequency distribution of treatment categories over year-classes. In the 2014 year-class the categories "hydrogen peroxide baths" and "combination" make up the main share of treatments, and a few experimental tests of thermal treatments. In the 2015 year-class non-medicinal treatments make up 75% of the total amount of treatments. The main share of treatments continues to be non-medicinal in the 2016 and 2017 year-classes.

The treatments took place in 159 unique farms in 10 of 13 production zones in Norway (Table 5). Treatment events are registered in production zone 1–9 and 11, but most of the treatments in the data are in production zone 3–7 (Table 5).

3.2 | Mortality

The N, mean, median, minimum, maximum and standard deviation of the mean for the baseline mortality Mrate within 7 days before treatment and ΔMrate within 1, 7 and 14 days after treatment for all six categories over years and year-classes are shown in Tables S1 and S2. There is a discrepancy in N between 1 and 7 to 14 days after treatment because the data set from one of the companies did not contain the number of dead one day after treatment, but rather the number of dead at treatment day. There is also a slightly different N between 7 and 14 days after treatment for thermal, mechanical and freshwater bath, because all fish in some cohorts were slaughtered between 8 and 14 days after treatment.

Figure 1 shows that the median ΔMrate for thermal treatment is the highest of all six treatment categories one and two weeks post-treatment. The median ΔMrate one day after treatment is highest for mechanical delousing. The median ΔMrate increases one week after thermal, hydrogen peroxide and freshwater treatment and then declines the following week. For mechanical, medicinal and combination treatment, the median ΔMrate has a slight decrease over the two-week period after treatment.

For all categories, the mean has a greater positive value than the median for all periods, which implies that there are some cohorts that experience very high mortality (positive outliers), contributing to a positive skewness (Tables S1 and S2). For example, in 2017 year-class (Table S2) the maximum ΔMrate two weeks after a thermal delousing was 0.0102928 compared to the median ΔMrate of 0.0003772.

For all six categories, the variability in ΔMrate is the highest for thermal, hydrogen peroxide and freshwater treatment. For all methods, the variability is reduced two weeks after treatment.

Further, we wished to explore if there has been a change in the ΔMrate over the past years and year-classes, especially for the newer delousing methods, thermal and mechanical. Here we have chosen to represent the change in number of treatments and ΔMrate both as yearly change (Figure 2) and as change over year-class (Figure 3). It is important to note that when looking at these results different year-classes, and thus size of fish, is represented in the different years.

For thermal treatments, the median ΔMrate shows a yearly decline from 2015 to 2018, followed by a rise in 2019 (Figure 2a). When looking at ΔMrate for thermal treatment over year-class (Figure 3a), there is a decrease from year-class 2014 to 2017. For mechanical delousing, there is an increase in median ΔMrate, both over the years (Figure 2b) and year-classes (Figure 3b). Hydrogen peroxide baths show no apparent pattern of change in the median ΔMrate over year (Figure 2c) and year-class (Figure 3c). For medicinal bath, the median ΔMrate declines with respect to both year (Figure 2d) and year-class (Figure 3d). For freshwater baths (Figure 2e), there is a decrease in median ΔMrate one and two weeks after treatment from 2016 to 2018. For combination treatment, there is an increase in the median ΔMrate over both year (Figure 2f) and year-class (Figure 3f). From year-class 2015 to 2016, this increase is pronounced; however, this is also the year-classes with the lowest N of this treatment method.

TABLE 3 Frequency of treatments within the different categories from year 2014 to 2019. The treatment category "Combination" contains combination of two different medicinal baths or combinations of hydrogen peroxide bath and medicinal bath. The data are gathered per year-class

	Year						
Delousing category	**2014***	**2015**	**2016**	**2017**	**2018**	**2019***	**Total**
Thermal	0	14	436	1 446	738	58	2 692
Mechanical	0	9	194	243	173	0	619
Hydrogen peroxide	29	297	49	41	29	0	445
Medicinal bath	1	94	33	16	54	0	198
Freshwater bath	0	6	54	87	25	0	172
Combination	16	452	40	10	0	0	518
Total	46	872	806	1 843	1 019	58	4 644

*Year 2014 represents only treatments of first year in sea of year-class 2014. Year 2019 represents only treatments of the last year in sea of year-class 2017. First treatment is in May 2014 and last in April 2019.

The average estimated weight of fish in the cohorts at the time of treatment ranged from 0.119 kg to 6.68 kg. Figure 4 shows box plot of the ΔMrate one week after treatment, over different weight-classes for different delousing methods. Thermally delousing salmon between 4-5kg and freshwater bath of salmon under 2kg have the highest median ΔMrate of all weight-classes and treatment methods. For freshwater baths of salmon under 2kg, the positive skewness and large positive variation imply some treatments with large mortalities. For thermal, mechanical and hydrogen peroxide treatment, the median ΔMrate rise for each kg up to 4kg.

3.3 | Actual numbers of dead fish due to treatment

Figure 5 shows the median ΔMrate transformed to the accumulated number of dead fish the first two weeks after delousing in a cage holding N0 = 150 000 salmon (close to the median population size in the data set which is 143 000). There is a variation in median mortality between the different delousing methods. In this study medicinal bath have the lowest and thermal treatment the highest median ΔMrate. When calculating mortality within two weeks after treatment using median ΔMrate of the 2017 year-class, 146/ 150 000 salmon died after medicinal delousing treatments, compared to 790 /150 000 after thermal and 928/150 000 after mechanical treatment of the same year-class. There is also a variation in median mortality between the year-classes within the same delousing methods. In 2014 year-class almost 4,000 salmon died within the first two weeks after thermal delousing, compared to 790 in the 2017 year-class.

TABLE 4 Frequency of treatments within the different categories from year-class 2014 to 2017. The treatment category "Combination" contains combination of two different medicinal baths or combinations of hydrogen peroxide bath and medicinal bath

	Year-class				
Delousing category	**2014**	**2015**	**2016**	**2017**	**Total**
Thermal	14	481	1 449	748	2 692
Mechanical	0	169	284	166	619
Hydrogen peroxide	324	52	32	37	445
Medicinal bath	114	13	21	50	198
Freshwater bath	5	55	85	27	172
Combination	419	91	8	0	518
Total	876	861	1 879	1 036	4 644

4 | DISCUSSION

The results show that we can expect elevated mortality after all of the six different delousing methods. There is variation in median delta mortality between the categories, where the overall median delta mortality after thermal and mechanical delousing is the highest of all methods. Median delta mortality decreases within two weeks after delousing, but not to the level before delousing for thermal, mechanical, hydrogen peroxide and freshwater treatments. Median delta mortality evolves differently between the delousing methods. We also find wide variability in delta mortality within the different delousing methods.

The results demonstrate that we can expect increased mortality after all six delousing methods (Figure 1), where the overall median delta mortality is the highest for thermal and mechanical delousing. This corresponds to the findings in a recent study done by Oliveira et al. (2021) where the most detrimental factor among all the mortality determinants analysed was the use of non-medicinal treatments for sea-lice.

The wide variability in delta mortality within, and variation between, the treatment methods could be associated with the delousing method itself, the health condition of the fish, environmental factors, or managerial factors at farm or company level.

All six delousing categories presented, require handling prior to treatment. Depending on method and duration of handling (crowding, pumping etc.), handling can cause stress, panic, injuries, decreased immunity and death (Ashley, 2007). Thus, the additional stress related to treatment handling, could itself cause increased mortality. If the delousing methods require different degrees of handling prior to treatment, this could explain some of the differences in mortality between methods. For example, farmers can delouse with hydrogen peroxide, medicinal and freshwater bath, in either cage or

TABLE 5 Frequency of treatments within the different categories over production zones in Norway. The treatment category "Combination" contains combination of two different medicinal baths or combinations of hydrogen peroxide bath and medicinal bath

	Production zone										
Delousing category	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**11**	**Total**
Thermal	47	207	272	523	398	790	272	133	19	31	2 692
Mechanical	1	3	16	7	54	337	125	62	7	7	619
Hydrogen peroxide	0	70	177	61	52	60	25	0	0	0	445
Medicinal bath	15	97	4	32	11	25	0	3	0	11	198
Freshwater bath	0	2	8	0	19	137	6	0	0	0	172
Combination	0	0	41	17	110	309	35	0	6	0	518
Total	65	380	522	654	669	1 672	465	205	34	49	4 644

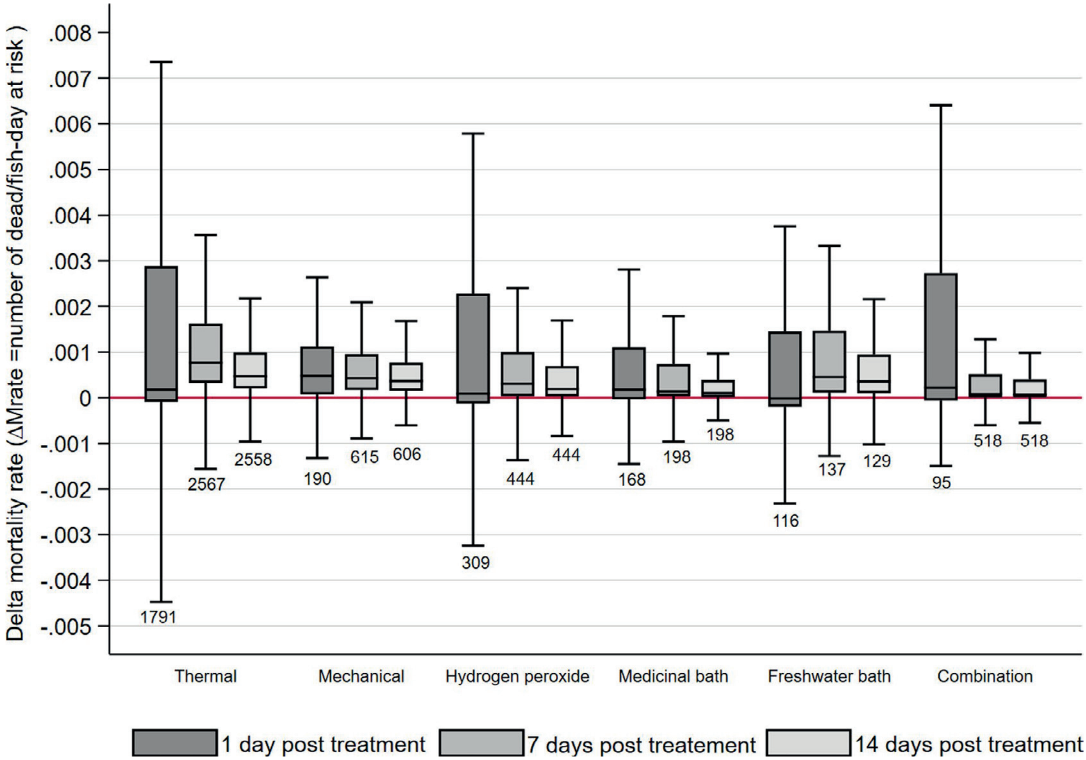

FIGURE 1 Boxplots showing delta mortality rate (ΔMrate) and its development 1, 7 and 14 days after six different categories of delousing treatments (thermal, mechanical, hydrogen peroxide, medicinal, freshwater and combination treatments). The treatment category "Combination" contains combination of two different medicinal baths or combinations of hydrogen peroxide bath and medicinal bath. The solid line within the coloured box indicates the median, and the coloured boxes indicate the ΔMrate of 50% of the treatments. The number beneath the box is *N* = number of treatments. The solid red reference line (ΔMrate = 0) shows mortality rate after delousing equal to the baseline mortality rate within 7 days before treatment. Note that the ΔMrate can be negative, which implies a reduction in mortality rate after delousing. The outliers are excluded from the visual presentation, but not the calculation

well boat. Performing a treatment in a well boat will require more handling than in-cage treatment.

Another explanation for the increased mortality after delousing and the differences in median delta mortality between the methods could be the degree of distress the delousing methods themselves inflict on the fish. In this study, both thermal and mechanical treatments have the highest median delta mortality. In a survey, fish health personal reported that they had experienced both thermal and mechanical treatments to cause a larger increase in mortality compared to medicinal and freshwater treatment (Hjeltnes et al., 2019). In the same survey, they also reported panic and episodes of poor water quality in treatment chamber and injuries after thermal treatment. In laboratory trials, exposing salmon to warm water caused rapid swimming and vigorous aversive reaction, a panic behaviour that can cause injuries in closed systems (Gismervik et al., 2019; Moltumyr et al., 2021; Nilsson et al., 2019). Less is known about how mechanical treatment affects fish. Gismervik et al. (2017), however, described industrial mechanical treatment having different effects on fish welfare and mortality, where a significant increase in bleeding from gills and scale loss were observed.

Regarding all delousing methods, median delta mortality generally decreases after two weeks, but not to the level it was prior to treatment. We also observed a difference between the delousing methods in progression of median delta mortality from one to 14 days after treatment. For thermal, hydrogen peroxide and freshwater delousing, the fish die with an increasing rate from day two to seven. The following week, the rate then declines. On the contrary, the median rate for mechanical, medicinal and combination treatment have a slight decrease within the first week and further decrease the following week. The reason for this delayed effect after treatment could be damages inflicted on the fish through handling and treatment method itself. In this study, treatments against only AGD are excluded. However, freshwater and hydrogen peroxide treatments are in some cases applied to treat against salmon lice and AGD at the same time. Thus, one explanation for the increasing mortality rate seen after hydrogen

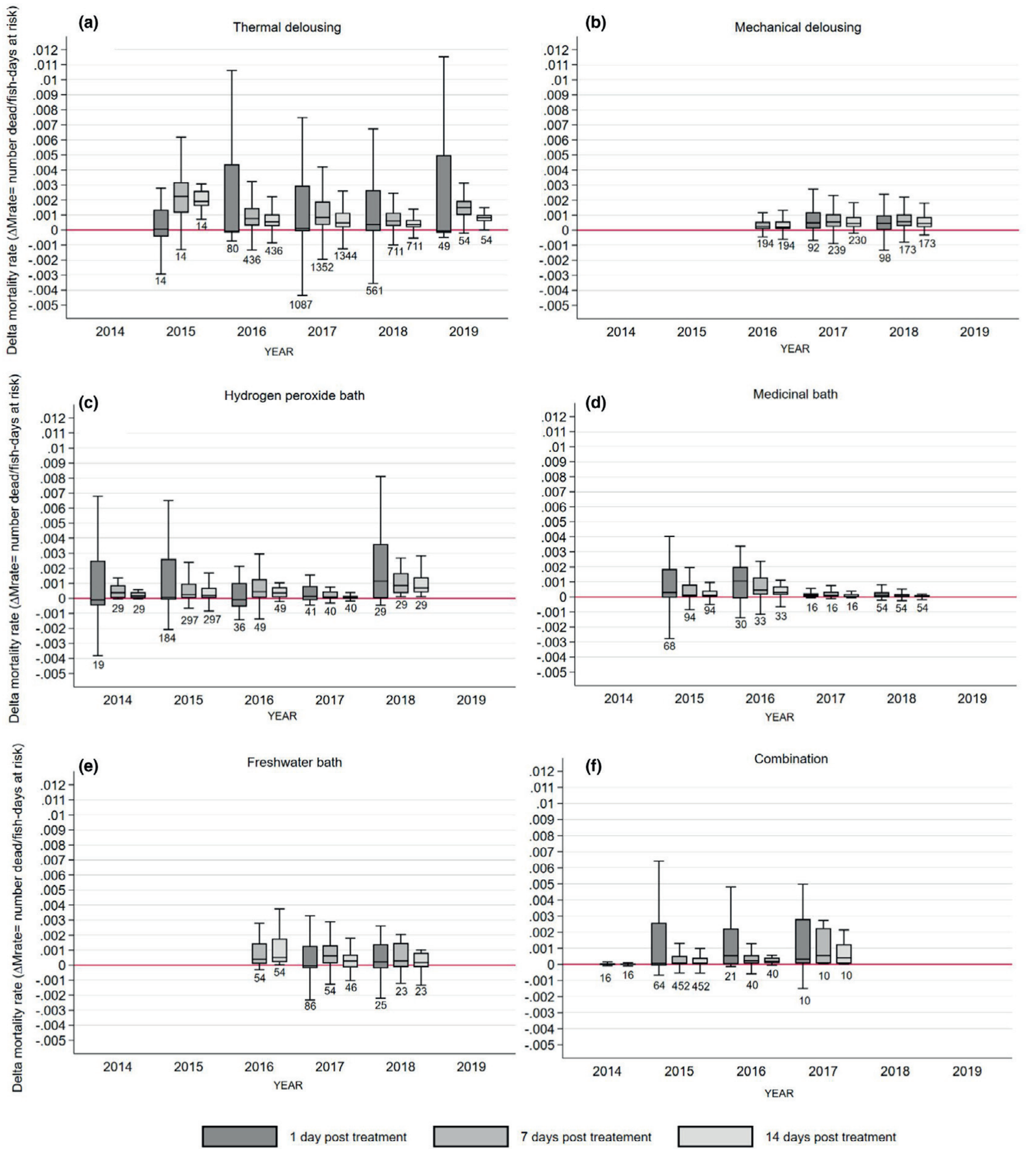

FIGURE 2 Boxplots show yearly change in delta mortality rate (ΔMrate) 1, 7 and 14 days after thermal (a), mechanical (b), hydrogen peroxide bath (c), medicinal bath (d), freshwater bath (e) and combination treatments (f). The treatment category "Combination" contains combination of two different medicinal baths or combinations of hydrogen peroxide bath and medicinal bath. Boxplots are made the same way as for Figure 1. The solid red reference line (ΔMrate = 0) shows mortality rate after delousing equal to the baseline mortality rate within 7 days before treatment. Categories with <10 treatments are not shown. The outliers are excluded from the visual presentation, but not the calculation

peroxide and freshwater could be poor gill health. Depending on the degree of poor gill health the mortality could be immediate or delayed.

For all categories, the mean delta mortality has a greater positive value than the median, which implies that there are some cohorts that experience very high mortality after delousing, contributing to a

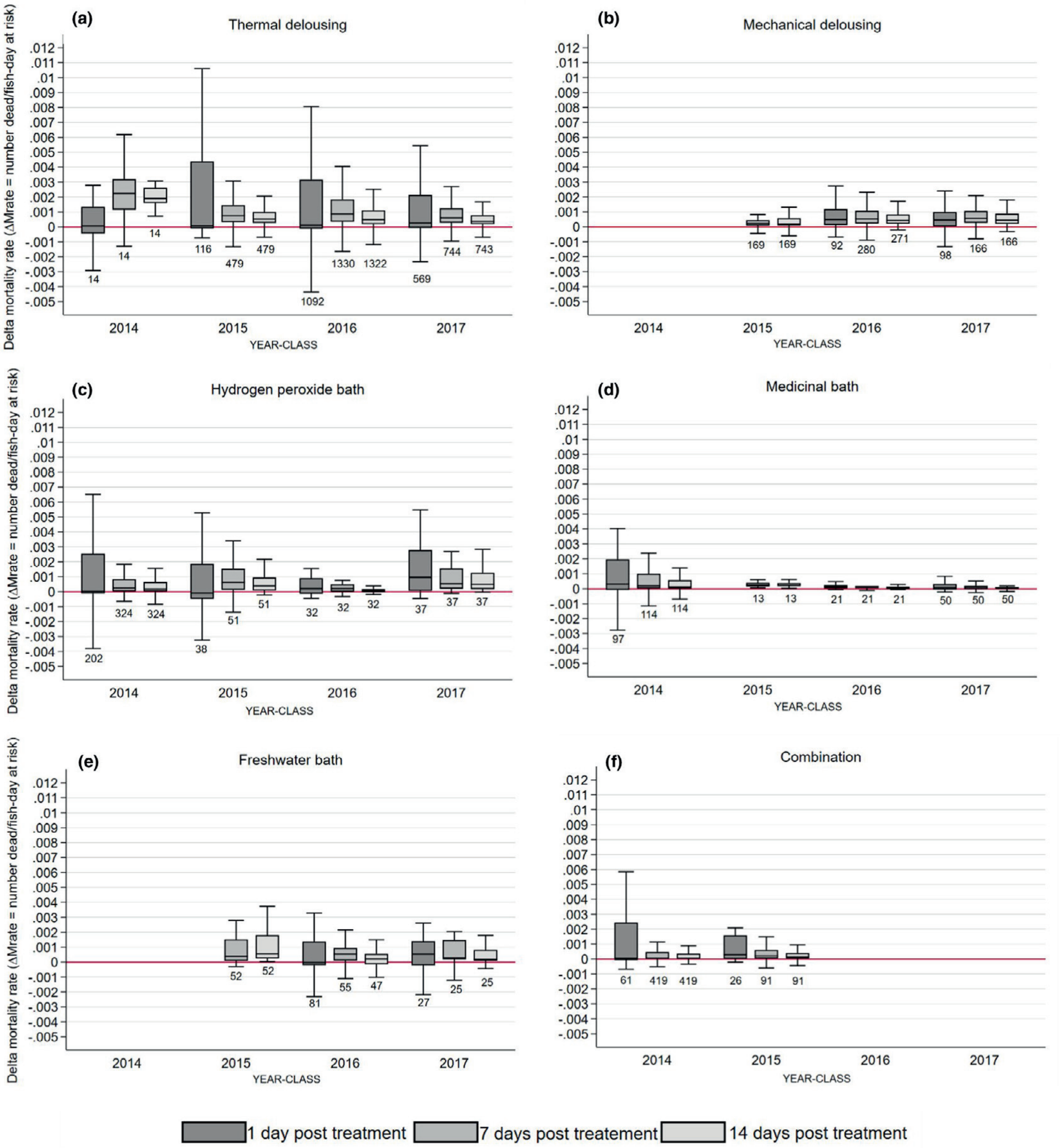

FIGURE 3 Boxplots show change over year-classes 2014–2017 in delta mortality rate (ΔMrate) after thermal (a), mechanical (b), hydrogen peroxide bath (c), medicinal bath (d), freshwater bath (e) and combination treatments (f). The treatment category "Combination" contains combination of two different medicinal baths or combinations of hydrogen peroxide bath and medicinal bath. Boxplots are made in the same way as for Figure 1. The solid red reference line (ΔMrate = 0) shows mortality rate after delousing equal to the baseline mortality rate within 7 days before treatment. Categories with < 10 treatments are not shown. The outliers are excluded from the visual presentation, but not the calculation

positive skewness. For example, in the 2017 year-class the maximum delta mortality rate after a thermal delousing corresponds to 19 961/150 000 salmon that died within two weeks after treatment. The median delta mortality rate corresponds to 790/150 000. The very high delta mortality and variability in mortality within the delousing treatments could be due to poor health/diseases, environmental factors (lack of oxygen), treatment failure, differences in skill and treatment rigs etc. Identifying such risk factors may prevent episodes of high mortality.

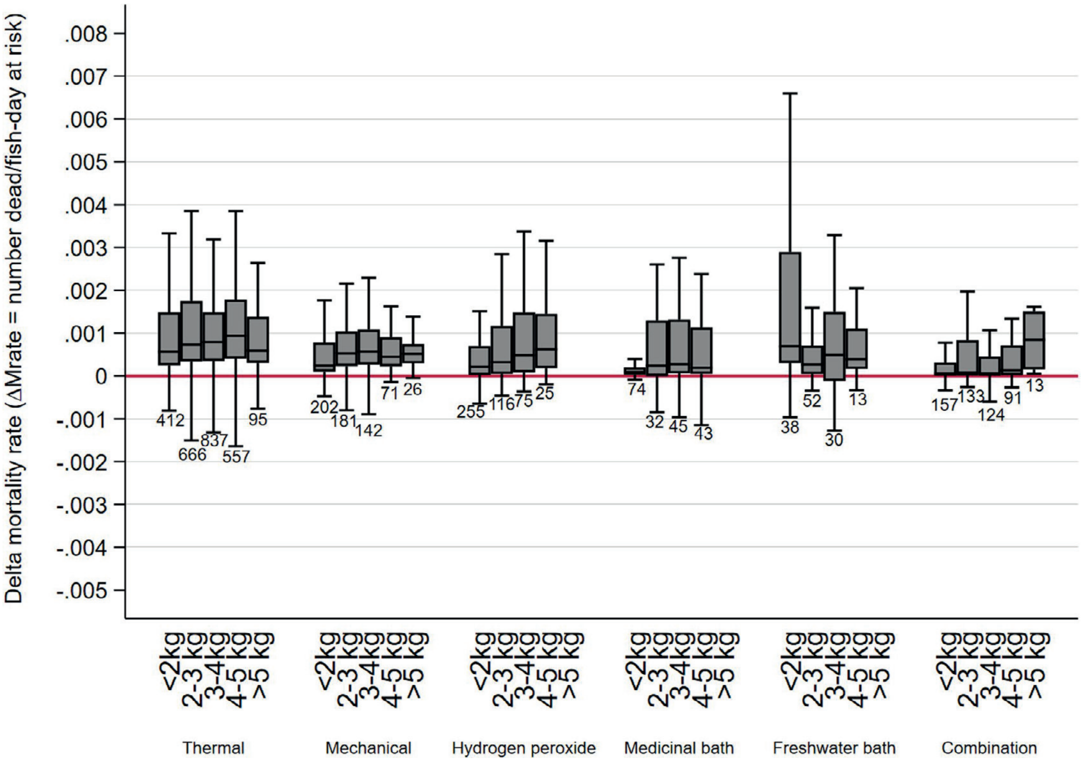

FIGURE 4 Boxplots show change over weight-classes: <2 kg, 2-3 kg, 3-4 kg, 4-5 kg and >5 kg in delta mortality rate (ΔMrate) 7 days after thermal, mechanical, hydrogen peroxide, medicinal, freshwater and combination treatments. The treatment category "Combination" contains combination of two different medicinal baths or combinations of hydrogen peroxide bath and medicinal bath. Boxplots are made in the same way as for Figure 1. The solid red reference line (ΔMrate = 0) shows mortality rate after delousing equal to the baseline mortality rate within 7 days before treatment. The outliers are excluded from the visual presentation, but not the calculation

An explanation for the variability in delta mortality within especially the newly introduced delousing methods could be improvements in knowledge, and management of treatment method. Implementing new methods is a continuous process of learning, evaluation and improvement. With increased experience, it is likely that technical equipment is adapted to decrease mortality after treatment. It is also likely that most companies have procedures to externalize experience made by farmers, related to for example handling or crowding fish prior to treatment. Regarding mechanical delousing, however, this study shows an increase in median delta mortality and no apparent change in variability in delta mortality over year (Figure 2) and year-classes (Figure 3). On the contrary, for thermal and freshwater treatment, we observe a decrease in both median and variability in delta mortality rate over the years and year-classes, with one exception. From year 2018 to 2019 there is an increase in median delta mortality after thermal treatment. Thermal treatment was introduced as delousing method in 2015, and we observe a yearly decrease in median delta mortality until 2018 and then an increase from 2018 to 2019. However, looking at change in delta mortality over year-class there is a consistent decrease from 2016 to 2017 year-class. It is important to remember this data set ends with the 2017 year-class. Therefore, 2019 represents only the second year of the 2017 year-class, which consist of mainly large fish, and this probably bias the results in year 2019. However, this increase in median delta mortality from year 2018 to 2019 might suggest that larger fish are more at risk of dying after thermal delousing. Therefore, we investigated delta mortality and fish weight.

The results of this study indicate that mortality increase with increasing weight up to 4 kg for all treatment methods, except freshwater. It is interesting that freshwater bath of salmon under 2 kg have one of the highest median delta mortalities. One explanation could be that subjecting salmon adapted to seawater to an abrupt transfer to freshwater will be more stressful to a young salmon (Powell et al., 2015). Salmon between 4-5kg that have been thermally deloused have the largest delta mortality within and between all treatment categories. Thus, difference in weight might explain some of the variability in delta mortality within the delousing methods.

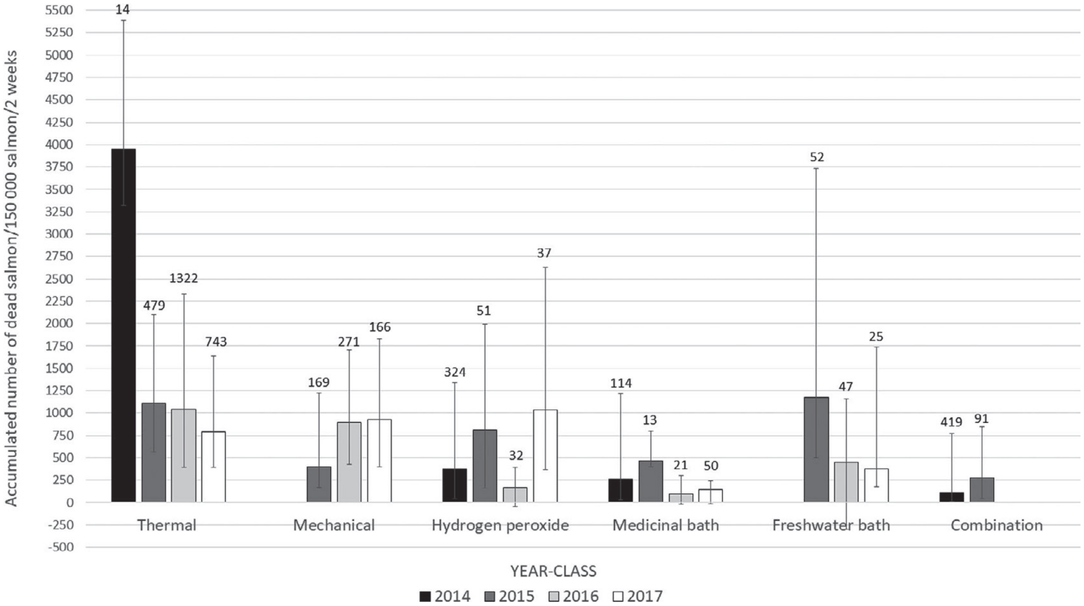

FIGURE 5 Accumulated number of dead fish 14 days after thermal, mechanical, hydrogen peroxide, medicinal bath, freshwater bath and combination of delousing treatments in an initial population of 150 000 before treatment. The treatment category "Combination" contains combination of two different medicinal baths or combinations of hydrogen peroxide bath and medicinal bath. The error bars show the interquartile range (25%–75%). Number above error bars are N = number of treatments. Categories with < 10 treatments are not shown

Weight increase with number of months in sea, and number of months are shown to be significant factors determining the level of mortality in sea phase aquaculture of salmonid fish (Bang Jensen, Qviller, et al., 2020). By examining mortality in cohorts slaughtered from 2014 to 2018, Bang Jensen, Qviller, et al. (2020) found that median mortality rate increased from the fourth to the 15th month across all years. Kilburn et al. (2012) found that mortalities due to pancreas disease are generally observed in larger fish (2-5kg), later in the production cycle. Risk of developing heart and skeletal muscle inflammation increased with increasing months at sea (Kristoffersen et al., 2013). Risk of developing cardiomyopathy syndrome increased with the number of days at sea (Bang Jensen et al., 2020). Thus, one possible explanation for median delta mortality increasing with increasing weight might be larger fish being more at risk of having these detrimental underlying diseases than younger fish.

Occurrence of underlying diseases that do not necessarily cause death unless extra stress is inflicted on the fish such as through delousing, can also explain variability in delta mortality after delousing. If health prior to treatment is poor, but mortality rate is low, this could result in a larger change in delta mortality after delousing, compared to a situation where prior treatment health is poor and mortality higher. Another explanation for the increased delta mortality in larger fish could be that these have been through several treatments, and there could be a build-up effect of repeated exposure to treatments.

Region (production zone) is also shown to be significant factors determining the level of mortality in sea phase aquaculture of salmonid fish (Bang Jensen, Qviller, et al., 2020). Regional variation in farm density and thus differences in host-density-dependent diseases might explain some of the variation seen in this study. Another explanation could be regional environmental differences, in for example sea temperature. Regional differences could also be one reason for the observed smaller variability in delta mortality after mechanical treatment compared to thermal treatment, as half of the mechanical delousing are in production zone 6. Preference could also be an explanation if mechanical treatment is only preferred in certain circumstances.

In this study, the most often used delousing methods are thermal (58%) and mechanical (13%). Variability and median delta mortality after thermal treatment has decreased from the 2015 year-class to the 2017 year-class, suggesting an improvement of the method. However, there is an increase in the number of thermal treatments from 14 in 2015 to 738 in 2018. Also, medicinal baths were the most commonly used delousing method until 2015 (Overton, Dempster, et al., 2018). If we compare medicinal baths to thermal treatment of the 2017 year-class, 146/150 000 salmon die within two weeks after medicinal bath. On the contrary, 790/150 000 and 928/150 000 salmon die within two weeks after thermally and mechanically treating the same year-class. This is a substantial increase. Also, if we use the median delta mortality for thermal treatment and the 2 692 thermal treatments in this data set, this adds up to over 2 million Atlantic salmon have died after thermal treatment from 2015 to 2019. This is a huge welfare and economic burden.

The present data set contains a large number of treatments for the most frequently applied delousing methods. The analysis of this data set also confirms the reported national yearly reduction of medicinal treatments and paradigm shift from medicinal to non-medicinal delousing treatments in Norway (Aaen et al., 2015; Helgesen et al., 2020; Myhre Jensen et al., 2020; Overton, Dempster, et al., 2018). The substantial increase in total number of treatments from year 2016 to 2017 (Table 3) and from year-class 2015 to 2016 (Table 4) is mainly due to missing production data from year-class 2015 and 2016 from one company. Since AquaCloud started registration of production data 01.01.2017, main part of production data from the 2015 year-class and the first year in sea from the 2016 year-class from one company is missing.

During the study period, the study population represents 214 farms (159 of them unique farms). In the period from 2014–2017 there were 717 active farms along the Norwegian coast (Oliveira et al., 2021), which means the data set represents about 22% of all active farms during that period. The data set might not reflect the actual distribution of treatments over production zones. There could also be differences in mortality between different companies and this may affect the mortality distributions presented here. Since the data from this study are only from large multi-farm companies, the results might not be representable for smaller companies. A recent study show that large (>20 locations) companies on average have a lower production loss (Pincinato et al., 2021). This does not necessarily imply that the described delta mortality in this study will be higher for smaller companies. Notably, in Pincinato et al. (2021), some of the best performing companies and farms were found in the group with the smallest companies.

The most important result from this study is the described wide variability and positive skewness in delta mortality, showing a potential for improvement. Compared to the other delousing methods the overall median delta mortality for thermal and mechanical delousing are the highest. Here, we have discussed if the wide variability in delta mortality within especially thermal treatment and variation between the treatment methods, can be associated with the delousing method itself, the health condition of the fish, environmental factors, or managerial factors. However, to make inference on causality more variables need to be included in the data set, and statistical modelling, such as multilevel regression would be required.

There is a growing concern regarding increasing mortality of farmed Atlantic salmon in Norway. If the numbers in the present study are explained by the delousing method itself and are representative for the entire Norwegian aquaculture salmon population, the shift from medicinal to non-medicinal delousing probably contributes to the overall increase in Norwegian salmon farming. Knowledge of both the effect from treatment measures and their side effects is important when deciding on treatment strategies. Salmon mortality is a direct negative effect of delousing. Few options for immediate delousing are available to the farmers, and the most commonly used methods cause higher mortality than the ones that previously dominated. Thus, finding the risk factors for mortality after thermal and mechanical treatments should be a top priority, together with alternative solutions of both managing and regulating salmon lice in Norway.

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CONFLICT OF INTEREST

None of the authors have any conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are subject to third party restrictions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Paper II

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How delousing affects the short-term growth of Atlantic salmon (*Salmo salar*)

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ABSTRACT

Infestations with salmon lice and subsequent salmon lice management is one of the most challenging and costly aspects of marine salmonid aquaculture. Both the handling and treatment, specifically non-medicinal treatment, against salmon lice cause stress and physical injuries to the host, the Atlantic salmon (*Salmo salar*). This in turn leads to reduced appetite and increased mortality. In this study, we have estimated the short-term growth loss of Atlantic salmon related to treatments (thermal, mechanical, hydrogen peroxide bath, freshwater bath and combination medicinal baths) for removal of salmon lice. To achieve this, we have obtained daily production data at cage-level from 2014 to 2019 from three large Norwegian aquaculture companies. We have used the registered feed-amount, number of fish and seawater temperature at cage level to calculate the thermal growth coefficient (TGC) of 635 fish-groups the week before a pre-treatment starvation period and the week after 2530 different treatments to estimate the reduction in TGC. We modelled this outcome using a mixed effect linear regression model, with treatment method as the main fixed effect of interest and fish weight, seawater temperature, smolt-age and year-class included as fixed effects. Results showed a period of suboptimal feeding and growth after all treatment methods, where non-medicinal treatment methods had a significantly larger negative effect on growth compared to medicinal treatments. The results also showed that timing of treatment played a role in the outcome of a treatment. The short-term biomass-loss in one cage following one non-medicinal treatment was estimated to 31,200 kg (average cage containing 150,000 fish weighing 3 kg, and seawater temperature of 10 °C). Thus, there could exist a potential for increased production in the Atlantic salmon aquaculture industry by reducing the number of delousing operations.

1. Introduction

Factors influencing growth are of great economic importance to the Norwegian salmonid aquaculture industry. For many years, infestations with salmon lice and salmon lice management have been one of the most challenging and costly aspects of Norwegian salmonid aquaculture, affecting both mortality and growth of Atlantic salmon.

Farmed Atlantic salmon live the first part of their lives in land-based freshwater sites. The fish are transferred to seawater sites in the fall the same year as they hatch (0-yearling), or in the spring the year after they have hatched (1-yearling). Groups of 150,000–200,000 salmon are stocked within open net-cages in seawater sites, where they live their on-growing period for about 1–1 ½ years until harvested. The sea-water sites are situated in one of 13 production zones on the Norwegian coast (NFD, 2017; Ådlandsvik, 2015).

The growth of Atlantic salmon is affected by several abiotic factors such as temperature, light, oxygen and salinity, and biotic factors such as fish size (age), access to and quality of feed and feeding regime (Brett, 1979). During the production at sea there is a substantial circannual and spatial variation in appetite and growth of Atlantic salmon, with a reduced growth during winter and increased appetite with increasing day-length (Aunsmo et al., 2014; Endal et al., 2000; Mørkøre and Rørvik, 2001; Nordgarden et al., 2003; Smith et al., 1993). Because Atlantic salmon is an ectothermic animal, appetite and growth are heavily

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influenced by temperature. Growth will increase with increasing temperatures up to a threshold of about 12-19 °C, and then decrease with further increasing temperature (Handeland et al., 2008; Hevrøy et al., 2012; Jobling, 1997). The appetite and growth of Atlantic salmon also depend on weight, and the daily percentage growth will decline as the fish increases in size (Austreng et al., 1987; Brett, 1979; Jobling, 1997).

Keeping track of daily weight gain and growth rate of the farmed salmon is an important part of the production, and companies can use several different models to estimate both weight gain and growth rate. The most important parameter when estimating daily weight gain is the amount of feed given to the fish. In Norway, salmon are fed by appetite and the farmers use cameras to stop feeding when the fish no longer eat. The appetite is evaluated by swimming behaviour and visible pellets at a prior set water depth. The daily weight gain will then be estimated by the amount of feed given, number of fish and the biological feed conversion ratio (bFCR). The bFCR is temperature and size dependent, and companies can use different models for estimating bFCR. There are also several different models for estimating the growth rate of salmon, and one of the most applied formula for calculating growth rate, that adjust for both temperature and size, is the thermal growth coefficient (TGC) (Cho, 1990; Iwama and Tautz, 2011).

Another important part of the production of Atlantic salmon is treatment of ectoparasites, such as salmon lice and *Paramoeba perurans* (causative agent of amoebic gill disease [AGD]). Treatment against salmon lice and AGD are common stressors for farmed Atlantic salmon. As stress negatively affects the appetite and growth of Atlantic salmon, occurrence of treatments might also explain a varying growth rate during production (Madaro et al., 2015; McCormick et al., 1998). Norwegian legislation requires that if the average number of adult female lice per fish per sea site exceeds a defined limit, farmers need to take measures to reduce the number of lice below the limit (NFD, 2012). Normally they do this by treatment. During the production at sea, most salmon are therefore treated at least once, but usually several times for ectoparasites, in particular salmon lice. A treatment operation at a site may involve one, several or all cages. Delousing treatments are either non-medicinal or medicinal. The non-medicinal treatments are categorized based on the principle of delousing method. The principle of thermal treatment is to inactivate the lice by exposing salmon with lice with heated water (maximum 34 °C) for up to 30 s (Grøntvedt et al., 2015; Overton et al., 2018; Roth, 2016). In mechanical delousing, the lice are removed by either brushing or flushing the lice off the fish (Gismervik et al., 2017; Nilsen et al., 2010). Freshwater treatment of salmon lice and AGD involves bathing the fish in low salinity water to inactivate the parasite (Powell et al., 2015). Thermal, mechanical and freshwater treatments are performed in well-boats or in treatment chambers in specialised rigs, which requires crowding and pumping of the fish. The medicinal treatments are administered via feed or by bath. The fish can be treated in cage or well-boat by bathing them in active substances such as azametiphos, cypermethrin, deltametrin or hydrogen peroxide. Crowding the fish is needed regardless of the type of bath treatment. Thus, handling the fish by crowding and/or pumping is an inherent part of both the non-medicinal and medicinal treatment. This is a major stressor which causes growth reduction (Delfosse et al., 2021; Erikson et al., 2016).

Since all treatments are performed in closed compartments (being either a well boat, treatment chamber, or tarp around the cage), there is a risk of the water-quality deteriorating when the water volume and water exchange is reduced compared to the normal cage environment. To decrease the risk of reduced water quality, the salmon are starved prior to treatment to reduce the amount of faeces during the operation (Einen et al., 1998). The number of days of starvation is determined by seawater temperature, size and health of the fish (Anonymous, 2020).

Because of increased resistance of salmon lice to medicinal compounds, thermal and mechanical delousing methods were introduced as non-medicinal substitutes around year 2015 (K. O. Helgesen et al., 2020; Overton et al., 2018). From 2015 to 2016, the industry rapidly shifted from medicinal to non-medicinal treatments (Overton et al., 2018). Currently, in Norway, the non-medicinal treatment operations are the most frequently applied methods for immediate removal of salmon lice (K. O. H. Helgesen et al., 2022). However, these non-medicinal methods negatively affect fish survival, and Persson and co-workers identified handling of fish and delousing operations to be the predominant causes of mortality during the marine production phase (Oliveira et al., 2021; Overton et al., 2018; Persson et al., 2022; Sviland Walde et al., 2021). Both mortality and suboptimal growth are indicators for reduced animal welfare and causes an economic loss to the farmers (Aunsmo et al., 2010; Stien et al., 2013). To reduce mortality and ensure optimal growth it is important to estimate the effects different management and environmental factors have on mortality and growth. We have previously showed that mortality after the most commonly used methods -thermal and mechanical- is many times higher compared to medicinal treatments (Sviland Walde et al., 2021). However, to the authors' knowledge there are no studies estimating the effect of different treatment methods on appetite and growth after a delousing treatment. The aim of this study was therefore to estimate the immediate effect different delousing methods have on growth of Atlantic salmon.

2. Material and methods

2.1. Data

Norwegian salmonid farming companies record data of their production, such as number of stocked fish, average fish weight, feeding (type and amount), mortality, treatments, salmon lice counts, environmental data etc. on cage-level (NFD, 2008). For this study, three large Norwegian Atlantic salmon farming companies (companies with >20 sites operating in multiple production zones) provided daily data from their production databases. The dataset used for this study was similar to the data utilized in the study described in Sviland Walde et al., 2021, but one exception: accumulated data from one company was replaced by daily data at cage-level covering the same sites and time period from that company (Sviland Walde et al., 2021). Two of the companies extracted the data directly from their production data monitoring system. Data from the third farming company was collected through Aquacloud, a digital database service within the Norwegian aquaculture industry (NCE Seafood Innovation, 2017).

The study population consisted of four year-classes (2014–2017) stocked in 279 unique sites. Year-class was defined as fish stocked within the same year. This corresponds to eight generations, with generations defined as fish stocked in either spring or fall within the same year (spring 2014-fall 2017). The smolt-age was denoted as years from the start of feeding to sea transfer, which would be either 0-yearling or 1-yearling. The study period started in spring 2014 and ended in fall 2019. Thus, the length of the study period allowed for production of more than one year-class at a specific site. Number of production cycles was defined as the number of year-classes per site during the study period. A fish-group was defined as fish within the same generation stocked at a sea site within the same cage. During the marine phase, groups of fish were often transferred between cages, and on occasion split or merged with other groups of fish, or had been moved to a different site. Therefore, we traced fish-group movements between cages from stocking until harvest. One observation (one row) in the dataset corresponded to one production day of one fish-group in one cage belonging to a specific year-class at a specific site in a specific production area.

2.2. Treatments

The main variable of interest for growth loss was treatment method. Based on information regarding treatment method, treatment indication and active substance (for medicinal treatments) supplied in the production data, treatments were categorized into eight categories as listed in Table 1. Both freshwater and hydrogen peroxide were used to remove the causative agent for the disease amoebic gill disease (AGD) *Paramoeba perurans* in addition to salmon lice. Because we wanted to look at the effect following treatments, excluding AGD-treatment could bias the results. We therefor included these AGD-treatments. However, the holding time in freshwater to treat AGD was substantially shorter compared to treatment against salmon lice (Holan et al., 2017; Hytterød et al., 2017). The concentration of hydrogen peroxide is also lower when treating against AGD compared to treating against salmon lice (Hytterød et al., 2017; Veterinærkatalogen, 2022). Therefore, we separated these two treatment methods into four different categories based on treatment indication. Information regarding whether treatments were performed in well-boat or in cage was not consistent in the data and therefore not included. Most of the current delousing methods require crowding and/or pumping, and we regard such handling as an inherent part of the treatment method. We did not expect delousing with medicinal feed to cause decreased feed intake (Veterinærkatalogen, 2022b), therefore treatment with medicinal feed was not included in this study. We gave each treatment event in a fish-group a treatment number according to the sequential order of treatments as indicated by the date of treatment supplied in the production data.

2.3. *Exclusion criteria*

The dataset consisted of 1,022,472 observations prior to filtering. Production data concerning other production types than that of Atlantic salmon for food consumption were excluded from the study data (151,713 observations). In addition, production data for the 2015 and 2016 year-class (159,439 observations) from one company were excluded because registration of production data started first of January 2017 in the digital database, Aquacloud. In some cases, production data had been recorded after a cage had been emptied, with the only information in these rows being the date, fish-group number and zero biomass. These rows were deleted (102,321 observations). Fish-groups were excluded if they were moved from one site to another, split or merged with other fish-groups, or impossible to trace (213,830 observations). We also excluded entire groups of fish that had less than seven days between two subsequent treatments (33,455 observations), as we regarded the first of these two treatments as failed, and the effect of each treatment impossible to separate. In addition, groups of fish with no treatment operation during the production cycle were excluded (54,859 observations). After we had excluded fish-groups based on the above-mentioned exclusion criteria, the dataset consisted of 306,855 observations, from 97 unique sites and 124 production cycles. In total, 635 fish-groups were treated 2530 times.

Table 1
Categories ($n = 8$) of immediate treatment operations applied in farmed Atlantic salmon in three Norwegian companies from 2014 to 2019.

Categories of treatment operations	Description of category of delousing operation
Thermal	Non-medicinal treatment using heated seawater. Includes all treatments using: a. Optilice ® b. Thermolicer c. Heated seawater
Mechanical	Non-medicinal treatment using brushing or flushing. Includes all treatments using: a. FLS Avlusersystem b. Hydrolicer c. SkaMik d. Flushing or mechanical treatment
Hydrogen peroxide	Hydrogen peroxide (H2O2) bath in pen or well boat against salmon lice
Medicinal bath	Medicinal bath in pen or well boat using one of the following active substances: a. Azamethipos b. Cypermethrin c. Deltamethrin d. Imidaclorid e. Other
Freshwater bath	Non-medicinal treatment using freshwater bath in pen or well boat against salmon lice
Combination medicinal	Medicinal treatment of the same cohort using the following two different combinations on the same day: a. two different active substances b. hydrogen peroxide and medicinal bath
Hydrogen peroxide AGD	Hydrogen peroxide (H2O2) bath in pen or well boat to treat amoebic gill disease (AGD)
Freshwater AGD	Freshwater bath in pen or well to treat amoebic gill disease

2.4. *Calculating and describing growth*

We estimated the daily weight gain and daily weight for each fish-group by eq. 1.1 and 1.2., and assumed all fish-groups converted feed with a fixed biological feed conversion rate (bFCR). The mean bFCR (=1.15) from one company was used as the fixed bFCR in the calculations. The recorded weight at first production day was defined as stocking weight. The close count was the number of fish in the fish-group at the end of the day. The feed amount was derived from the production data as kg/day/cage.

$$\text{Daily weight gain } [\text{g}] = 1000^{*}(\text{feed amount } [\text{kg}]/\text{close count}/\text{bFCR}) \tag{1.1}$$

$$\text{Estimated daily weight } (\text{w}_\text{t})[\text{g}] = \text{stocking weight} + \sum_{i=1}^{n} \text{daily weight gain} \tag{1.2}$$

n = number of production days.

As a measure of growth rate, we applied the formula for thermal growth coefficient (TGC) (Cho, 1992), and calculated the daily TGC for each fish-group by eq. 1.3. The end weight (*weight end)* was the estimated daily weight derived from eq. 1.2, and the starting weight (*weight start)* was the estimated weight the day before. Since we calculated the daily TGC, day degrees (DG) was equal to the daily registered seawater temperature. Daily temperature registrations were occasionally missing. In cases of missing temperature for scattered single days, the mean temperature was imputed from the temperature registered the day before and after. In a few cases, more than one week of coherent temperature-registrations were missing. Such cases were handled by assigning the corresponding weekly sea temperature for the site registered in the public database Barentswatch (www.barentswatch.no). If the weekly temperature was missing in Barentswatch, the temperature was linearly interpolated (extrapolated) using the command "epolate" in Stata (StataCorp, 2017a).

$$\text{daily TGC} = \frac{1000\ (\text{weight end})^{1/3} - (\text{weight start})^{1/3}}{\text{DG}} \tag{1.3}$$

$$\text{baseline TGC} = \sum_{i=1}^{n=5} \frac{\text{daily TGC}_{\text{pre-treatment starvation i}}}{\text{n}} \tag{1.4}$$

A treatment event was normally initiated by a period of starvation. We defined starvation as daily feed amount equal to zero in the production data. Due to daily variations in the TGC, we calculated the mean of the daily TGC for each fish-group during the last five days before a starvation related to a treatment event, and used this as a baseline (eq. 1.4). To reduce the risk of including a period of starvation from an earlier treatment in the baseline TGC, the period for calculating the baseline was restricted to maximum 14 days prior to the day of treatment. We subtracted the baseline TGC from the calculated daily TGC to find the daily change in TGC (daily ΔTGC) after treatment (eq. 1.5).

$$daily\ \Delta TGC = daily\ TGC\ post\ treatment - baseline\ TGC \tag{1.5}$$

We presented the distribution of daily ΔTGC over a 14-day period after a treatment event in the form of Tukey Box plots. Data management, descriptive statistics and statistical analysis were performed in the statistical software package Stata ® SE 15.1 (StataCorp, College Station, Texas USA) and in Microsoft ® Office Excel.

2.5. *Statistical analysis*

2.5.1. *Outcome variable*

The outcome variable in the statistical modelling was the mean of the daily ΔTGC seven days post treatment (abbreviated to ΔTGC) (eq. 1.6). The baseline comparison was thus the five day mean TGC prior to each treatment of each fish-group (eq. 1.4). The distribution of the outcome variable was visually assessed by histogram and box plots.

$$\Delta \mathrm{TGC} = \sum_{\mathrm{i}=1}^{\mathrm{n}=7} \frac{\mathrm{daily}\ \Delta\ \mathrm{TGC_i}}{\mathrm{n}} \tag{1.6}$$

2.5.2. *Explanatory variables*

In addition to the main explanatory variable of interest -treatment method- we selected other available production parameters in the dataset that could have a biological rationale for affecting growth. These were variables that described treatment (seawater temperature at treatment, number of days starved prior to treatment, treatment sequence number, number of weeks between treatments and treatment year), variables describing fish-groups (year-class, generation, smolt-age, weight at treatment), temporal variables (number of days and day-degrees from stocking to treatment, season, month and year) and spatial variables (production area and latitude).

The interaction between the explanatory variables and the outcome were assessed by building casual diagram using directed acyclic graphs (DAGitty v3.0), and by univariable analysis. We selected explanatory variables to be included in the final model building if they were regarded as possible confounders (guided by literature review and the casual diagram), or the *p*-value was below 0.2 in the univariable analysis. Some of the explanatory variables contained essentially the same information, and to avoid multicollinearity we selected which explanatory variable to be included in further model building based on criteria of biological plausibility and reliability of measurement.

2.5.3. *Data structure and multivariable statistical model*

To account for the clustered nature of production data, statistical modelling was performed with a mixed effect linear regression model with random intercepts using the mixed command in Stata (StataCorp, 2017b).

Different unconditional models (model without fixed effects) were tested, and the model with the most sensible biological rational clusters, highest intraclass correlation coefficient (ICC) and lowest AIC was selected as final unconditional-model. Interclass correlation coefficient (ICC) for each level was calculated as described in Rabe-Hesketh and Skrondal, 2008 (Rabe-Hesketh and Skrondal, 2008).

We included the fixed effects (explanatory variables) using a forward stepwise model building procedure, and variables were kept in the model if they were assessed as possible confounders and/or the p-value was below 0.01. The simplest model with the lowest AIC was preferred.

The residuals were visually assessed for the assumption of normality by q-norm and histogram plots and homoscedasticity by scatter plots. The reliability of the model was tested by randomly splitting the data in half, and the final mixed effect linear model was run on both halves.

The statistics calculated from both the overall estimation of the fitted mixed effect model and with specified values for the fixed effects (estimated margins) were graphically presented using the margins plot command in Stata. (Willams, 2012). A post hoc pairwise comparison across the levels of the treatment categories from the fitted model was done using the Stata margins command “pwcompare” (StataCorp, 2017c).

2.6. *Calculating losses in grams*

To provide an example of what the absolute number of weight gain loss in grams related to an individual treatment could be, we applied the estimated means for treatment method from the mixed effect linear regression to calculate the potential loss in grams per fish (eq. 1.7–1.11). The estimated mean was adjusted for weight category of 3-4 kg, temperature of 10 °C (i.e. the optimal growth temperature), and year-class of 2017. We calculated the end weight in a 14 day period for a standardized fish weighing 3 kg before treatment (weight start), being starved for 7 days (eq. 1.7), set the TGC prior treatment of 3.5 and added the adjusted estimated ΔTGC to calculate the end weight seven days after an individual thermal, mechanical and medicinal treatment (eq. 1.8). We compared the weight gain (eq. 1.10) of the standardized treated fish with a standardized fish of 3 kg, growing at a constant TGC of 3.5 the entire 14-day period (eq. 1.9) to find the difference (loss) in weight gain (eq. 1.11) for the treated fish vs. the non-treated fish. We could then estimate the potential growth loss for an average cage (eq. 1.12) and site (eq. 1.3).

$$weight_{end\ 7\ days\ starv} = \left[(\mathrm{weight_{start}})^{\frac{1}{3}} + \frac{\mathrm{TGCstarv} = 0}{1000} * (DG) \right]^3 \tag{1.7}$$

$$weight_{end\,7\,days\,post\,treat} = \left[(\mathrm{weight_{end\,7\,days\,starv}})^{\frac{1}{3}} + \frac{\mathrm{TGC\,prior\,treat} + \Delta\mathrm{TGC}}{1000} * (DG) \right]^3 \tag{1.8}$$

$$weight_{end\ no\ treat} = \left[(\mathrm{weight_{start}})^{\frac{1}{3}} + \frac{\mathrm{TGC\ prior\ treat}}{1000} * (DG) \right]^3 \tag{1.9}$$

$$weight\ gain = weight_{end} - weight_{start} \tag{1.10}$$

$$growth\ loss\ per\ fish = weight\ gain_{no\ treat} - weight\ gain_{treat} \tag{1.11}$$

$$growth\ loss\ per\ treat\ per\ cage = growth\ loss\ per\ fish^{*}\ number\ of\ fish\ in\ cage \tag{1.12}$$

$$growth\ loss\ per\ treat\ per\ site = growth\ loss\ per\ treat\ per\ cage^{*}\ number\ of\ cages\ per\ site \tag{1.13}$$

3. Results

3.1. *Data*

There were 717 active sites along the Norwegian coast during 2014–2019 (Oliveira et al., 2021). This dataset thus represented 13.5% of all active sites in the study period. Table 2 shows the overall frequency distribution for the eight different categories of salmon lice treatments

Table 2
Frequency distribution of treatment categories over year-classes (after applying exclusion criteria as explained in section 2.3).

	Year-class				
Treatment category	2014	2015	2016	2017	Total
Thermal	10	248	316	485	1059
Mechanical	0	99	133	122	354
Hydrogen peroxide	237	35	0	36	308
Medicinal bath	106	9	1	40	156
Freshwater bath	2	26	4	16	48
Combination medicinal	285	70	2	4	361
Hydrogen peroxide AGD	111	42	20	4	177
Freshwater AGD	6	4	4	53	67
Total	757	533	480	760	2530

over year-classes. The first treatment event took place May 2014 and the last in April 2019. More than half of all treatments were non-medicinal, where the main share were thermal treatments. The medicinal treatments mainly consisted of hydrogen peroxide and combinational treatments. A shift from medicinal to non-medicinal treatments dominating occurred between the 2014 and 2015 year-class (Table 2).

Table 3
The range and number of clusters at each level in the data structure. "Treatment sequence number" is number of clusters of fish-groups within the same site having the same treatment number. Treatment event is the cluster of treatments of fish-groups within the same site having the same treatment number.

			Number of clusters at level above	
	Level	Number of units	Mean	Range
Data structure	Site	97	–	–
	Treatment sequence number	571	5.8	1–11
	Treatment event	2530	4.4	1–18

3.2. Change in growth rate after treatment

The overall daily change in TGC 14 days after the 2530 treatment events is shown in Fig. 1 A. The median value for the daily change in TGC returned to the baseline level, i.e., the same appetite and growth rate as before starvation, after seven days. The greatest variation in the

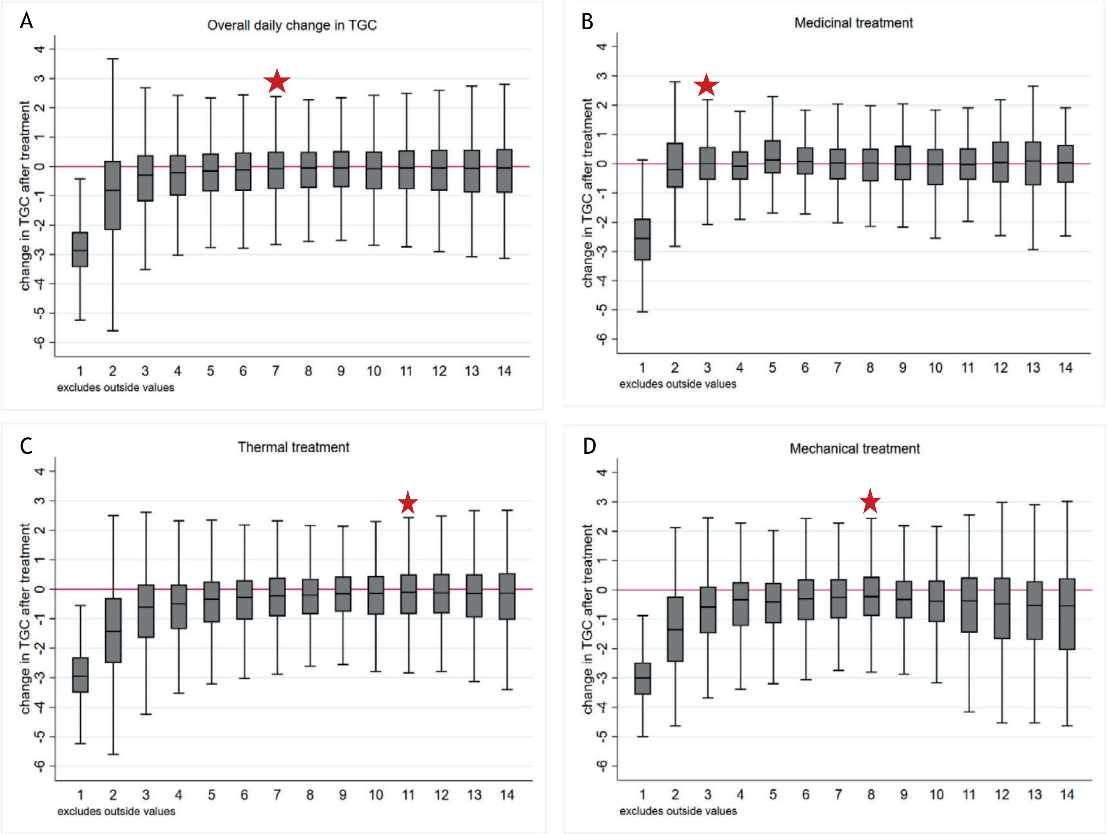

Fig. 1. Box plot showing change in daily thermal growth coefficient (TGC) 1–14 days after a treatment event overall for all treatments (A) and for medicinal (B), thermal (C) and mechanical (D) treatment. The red reference line indicates no change in TGC (=0) after treatment. A negative change in daily TGC thus indicates a reduction in the appetite and growth rate compared to the baseline TGC (given by the mean of daily TGC over a five-day period before starvation and treatment). The star shows the first day the median change in daily TGC is closest to the baseline TGC. Any outliers are excluded from the visual presentation, but not from the calculations of the box plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

daily change in TGC occurred at day 2. The daily change in TGC specifically for medicinal bath, thermal and mechanical treatment is shown in Fig. 1 B—D. For medicinal treatment, the daily change in TGC was back to baseline level after three days (Fig. 1B), whereas for thermal treatment this took about eleven days (Fig. 1C). For mechanical treatment, the daily change in TGC was closest to baseline level after eight days (Fig. 1D).

3.3. Statistical analysis

The outcome for the statistical analysis was the mean of daily change in TGC in a seven-day period after a treatment event (ΔTGC). The outcome was normally distributed (mean = −0.726, maximum = 4.38 and minimum = −3.98).

3.3.1. Data structure

In Table 3, the final clustering of the data structure is described with mean and range of clusters per level above. In this dataset, when a treatment within a site was initiated, normally all fish-groups within the site were treated. This meant that when a treatment at a site occurred, most of the fish-groups that were treated had the same number of previous treatments, and approximately the same number of days had elapsed since the last treatment. The number of days between treatments of the different fish-groups within a site were on average 8 days, median 1 day apart. In the final structure, a site had on average 5.8 treatments, and when a treatment at a site was initiated, an average of 4.4 different fish-groups were treated, within an average 16-day (median 4-day) period. The cluster "treatment sequence number" was the treatment number for each fish-group within the same year-class and site. The final structure thus defined clusters of fish group within the same site where most of the fish-groups within the cluster "treatment sequence number" had been treated temporarily close in time and had the same previous amount of treatments.

We excluded production cycle and production area as levels, as there were too few production cycles within a site, and the variance of number of sites within production area were high. Within a site, there was a moderate correlation (ICC = 0.503) of the outcome of treatments performed averagely within the same month, median within the same week on different fish-groups sharing the same amount of previous treatments.

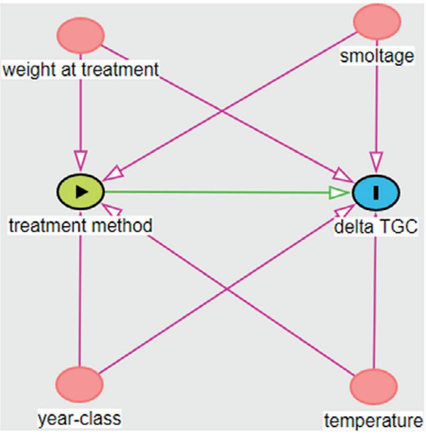

Fig. 2. A directed acyclic graph showing the proposed associations between the selected fixed effects and outcome (blue circle). We want to know the effect of treatment method (green circle) on growth rate, expressed as ΔTGC (blue circle) and adjust for the factors shown in red circles. The arrowed lines indicate casual path and their directions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3.2. Factors affecting change in growth after treatment

Descriptive statistics as number of treatment events per level for categorical values, and mean, median and range for continuous variables, in addition to the association (*p*-value) with the outcome variable (univariable analysis) for all potential explanatory variables are shown in Table A.1. The mean temperature at treatment day was 9.6 °C (median 9.2 °C, minimum 2.3 °C and maximum 19.2 °C).

3.3.3. Statistical model and estimations

The final model included the following fixed effect variables: treatment method, weight at treatment, year-class, smolt-age and temperature. Fig. 2 shows that year-class, weight at treatment, smolt-age and temperature were considered as confounders.

The full mixed effect linear regression model with both the fixed and random effects is shown in Table 4. There was a random intercept for site and treatment sequence number. The ICC at site level was 0.045, which meant there was 4.5% correlation between treatment events within the same site. However, there was 41% correlation between treatments of different fish-groups within the same site, with the same treatment sequence number. When including the fixed variables to the model, the total variance accounted for about 16% (R^2). For the proportion of the variance of the full model, 59% lied between treatments of different fish-groups within the same site, 37% between following treatments within

Table 4
Fixed and random effects in the fitted mixed effect linear model where outcome is change in TGC after treatment event. Coeff = coefficients, SE = standard error, CI = confidence interval, prop. Var. = proportion of the variance between levels, ICC = intracluster correlation. Treatments, weight-classes and year-classes sharing the same superscript letter are not significantly different at the 5% level.

	Coeff.	SE	95% CI		p-value	
Intercept	−0.777	0.147	−1.07	−0.49	<0.001	
Fixed effects						
Treatment method					<0.001	
Medicinal (baseline)^{c}						
Thermal^{a}	−0.415	0.111	−0.63	−0.20	<0.001	
Mechanical^{a}	−0.394	0.121	−0.63	−0.16	0.001	
Hydrogen peroxide^{bc}	−0.088	0.109	−0.30	0.13	0.419	
Freshwater bath^{ab}	−0.365	0.160	−0.68	−0.05	0.023	
Combination^{c}	0.059	0.112	−0.16	0.28	0.597	
Hydrogen peroxide AGD^{bc}	−0.136	0.138	−0.41	0.13	0.323	
Freshwater AGD^{bc}	−0.063	0.163	−0.38	0.26	0.699	
Weight					<0.001	
<1 kg (baseline)^{b}						
1–2 kg^{b}	−0.067	0.066	−0.20	0.06	0.309	
2-3 kg	−0.159	0.071	−0.30	−0.02	0.025	
3–4 kg^{a}	−0.363	0.075	−0.51	−0.22	<0.001	
>4 kg^{a}	−0.307	0.080	−0.46	−0.15	<0.001	
Yearclass					<0.001	
2014 (baseline)^{a}						
2015	−0.379	0.104	−0.58	−0.17	0.002	
2016^{a}	−0.134	0.110	−0.35	0.08	0.031	
2017^{a}	−0.019	0.104	−0.22	0.18	0.733	
Smoltage					0.009	
1-yearling (baseline)						
0 yearling	0.159	0.061	0.04	0.28	0.009	
Temp	0.052	0.007	0.04	0.07	<0.001	
Random effects	Estimate	SE	95% CI		Prop. var	ICC
Site	0.172	0.042	0.107	0.279	0.045	0.045
Treatment sequence number	0.492	0.023	0.448	0.540	0.367	0.412
Residual	0.622	0.010	0.603	0.642	0.588	

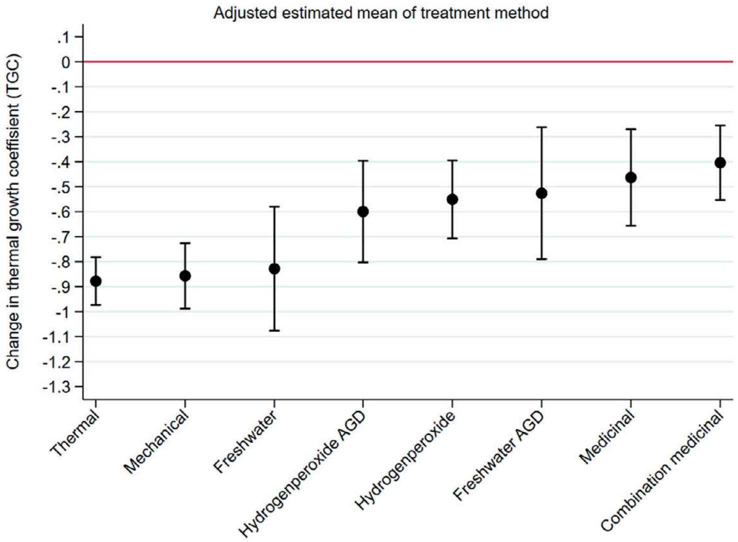

Fig. 3. Graph showing the estimated mean of the change in thermal growth coefficient (ΔTGC) from the fitted mixed effect linear regression model. The black circle for each treatment method represents the average value of the ΔTGC. The bars indicate 95% confidence intervals. The red reference line indicate the baseline TGC (given by the mean of daily TGC over a five-day period before starvation and treatment) and is equal to no change in TGC (=0) after treatment. A negative change in ΔTGC indicates a reduction in the appetite and thus growth rate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the same site, and only 4.5% between different sites.

Treatment method had a significant negative effect on the change in growth rate seven days after treatment (Table 4 and Fig. 3). The post hoc pairwise comparison showed thermal, mechanical and freshwater treatments differed significantly from the baseline (medicinal treatment), with a larger effect of −0.415, −0.395 and − 0.365, respectively (Table 4 and Fig. 3).

The post hoc pairwise comparison also showed that the negative effect of the 2015 year-class were significantly different from the 2014 year-class, however the negative effect of year-classes decreased from 2015 to 2017, and were no longer significantly different compared to 2014 (Table 4). When fish exceeded three kg in weight, there was a significant negative effect on the change in TGC, compared to when the fish was under one kg (Table 4). 1-yearlings had a lower change in TGC compared to the 0-yearling (Table 4) and higher seawater temperature showed a positive effect on the change in TGC (Table 4).

When splitting the dataset randomly in two halves, the output of the final mixed effect linear regression model gave the same trends as for the entire dataset, except for freshwater treatments against salmon lice.

3.4. Calculating losses in grams

The estimated potential weight gain loss per fish seven days after treatment was highest for thermal (52.5 ± 6.0 g) and mechanical (51.5

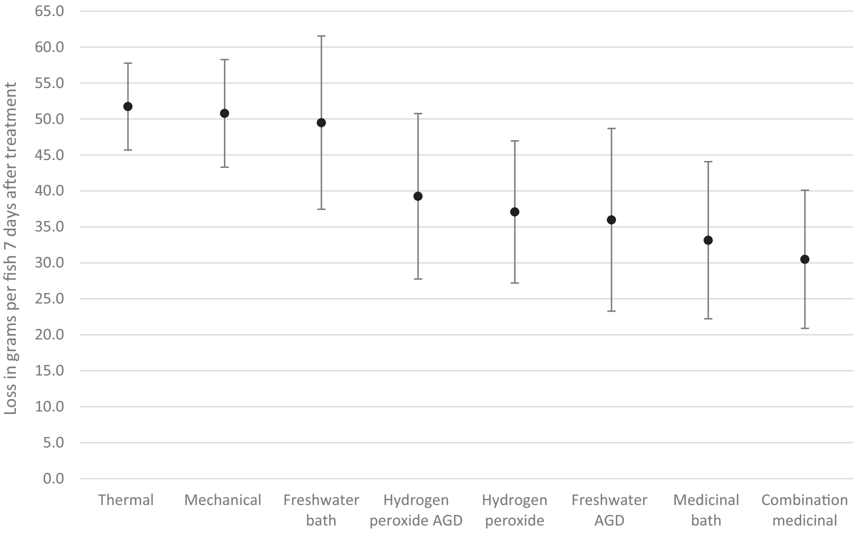

Fig. 4. Loss in weight (grams/per fish) related to each type of treatment method, when treating a standardized fish weighing 3 kg at a seawater temperature of 10 °C (i.e. the optimal growth temperature). The bars show the 95% confidence interval.

Table 5
The estimated weight gain for a fish-group from the 2017 year-class, treated at 3 kg at 10 °C seawater temperature. These figures are based on the post estimation from the mixed effect linear regression shown in Fig. 4. The 14-day period is divided into a 7-day period of starvation and the following 7-day period after a non-medicinal treatment. The treated fish-group is compared to a fish-group with the same starting weight of 3 kg and growing with a constant TGC of 3.5 at 10 °C.

	Estimated weight gain per fish	
	Non-medicinal treatment	No treatment
Pre treatment starvation period (7 days)	0 g	155
Post treatment weight gain (7 days)	52 ± 7.5 g	161
Total weight gain (14 days)	108 ± 7.5 g	316
Difference non-medicinal treatment vs non-treatment 7-day period post treatment	52 ± 7.5 g	
Difference non-medicinal treatment vs non-treatment 14-day period	208 ± 7.5 g	

± 7.5 g) treatments (Fig. 4).

Table 5 shows the estimated weight gain for a fish-group from the 2017 year-class, treated at 3 kg at 10 °C seawater temperature based on the post estimation from the mixed effect linear regression shown in Table 4 and Fig. 3. Thermal and mechanical treatments reduced the growth the week after treatment with about 52 g per fish compared to a non-treated group (Table 5). When a period of starvation of seven days was included, this added up to an average loss of 208 g per fish. About 25% of the loss in a two-week period was due to suboptimal growth the week after treatment, and the remaining 75% was due to the period of starvation prior to treatment. In this dataset, the average number of fish in a cage at treatment date was approximately 150,000 and average number of fish-groups (i.e. cages) per site 5. Thus, seven days of starvation and seven days of suboptimal appetite after a non-medicinal delousing operation, added up to a potential weight gain loss of about 31,200 kg of biomass per cage per non-medicinal treatment, corresponding to 156,000 kg biomass per site per non-medicinal treatment.

4. Discussion

The results from this study showed a significant negative effect of treatment against salmon lice and AGD on the mean change in TGC 7 days after treatment (Table 4 and Fig. 3). Thermal, mechanical and freshwater treatments against salmon lice had a significantly larger negative effect, compared to medicinal treatments (Table 4 and Fig. 3). The main source of the unexplained variation was attributed to the actual treatment event and there was a moderate correlation of the outcome of treatments within the same site, when treatments were performed close in time (Table 4).

4.1. Measurement of growth

The TGC is a widely used formula for predicting growth in production planning, since it adjusts for both seawater temperature and size of fish. TGC has been shown to be independent of temperature within a temperature range of 7.5-16 °C (Jobling, 2003). However, outside this range, the TGC will give erroneous results (Jobling, 2003). Temperature at treatment day approximated a normal distribution in this dataset, with a mean of 9.6 °C, and a range of 2.3–19.2 °C. Thus, the main share of the observations were within the area where TGC is a suitable measure for growth.

In addition to temperature and size, several unmeasured spatial and temporal factors influences growth both within and between fish-groups, such as occurrence of disease, seasonal variations, breed and environmental differences (light, water quality etc.). These factors are not adjusted by the TGC. To correct for the erroneous results obtained for the observations outside the temperature range for TGC, and to some extent try to adjust for these unmeasured factors, we applied the mean change in TGC in a 7-day period after treatment (ΔTGC) as the outcome for the mixed effect linear regression. If the ΔTGC was equal to zero, this implied the same growth rate the week after treatment as the growth rate the week before the pre-treatment starvation period (baseline TGC) began. A negative ΔTGC implied a lower growth rate the week after treatment compared to the baseline.

To calculate the daily TGC the biological feed conversion ratio (bFCR) is necessary. The true bFCR was not known since bFCR is an estimated value in the production data. In addition, the bFCR models used by different companies vary. Therefore, a simple approach was used where the same bFCR was assumed for all fish-groups during their entire production cycle. This approach did not adjust for the size dependency of bFCR and could cause a small underestimation of the treatment effect on growth.

It is also possible that the feed amount did not perfectly reflect the appetite of the fish. However, this was largely accounted for by analysing the change in growth rate. In addition, since feed constitutes for about 50% of the production cost (Iversen et al., 2017) the farmers have a strong incentive for reducing feed-spill.

One disadvantage of using the change in TGC as an outcome variable was that we might have adjusted for effects related to the prior treatment. This matter was reflected in the univariable analysis when we added weeks between treatments as a fixed effect (Table A.1). In this model, decreasing the number of weeks between treatments showed a positive effect on the ΔTGC after treatment (Table A.1). This made no sense, as the fish would have less time to recover from the last treatment. The reason for this became apparent when the outcome variable was changed from ΔTGC to baseline TGC in a univariable analysis with weeks between treatment as fixed effect (Table A.2). This analysis showed a significant reduction in the baseline when there was less than two weeks between two following treatments (Table A.2). This indicated an additive effect of treatments closer than two weeks. In addition, it showed that the negative effect on the baseline most likely lead to a decrease in ΔTGC, since decreasing number of weeks had a positive effect when the outcome variable was ΔTGC. Even if the variable “weeks between treatment” was statistically significant, it could not be added as an explanatory variable to the full model, because it caused a false positive effect in the estimation of ΔTGC.

In this dataset there were few freshwater treatments against salmon lice ($n = 48$). When the reliability of the dataset was tested by split-sample analysis, the above mentioned was probably the reason why freshwater treatments were not significantly different from medicinal treatment. We found this to be true in one of the split-samples, opposed to the results from the other sample, and the full dataset.

4.2. The effect of treatment methods on growth

The aim of the study was to estimate the effect of different treatments on growth rate after a treatment event.

As the causal diagram (Fig. 2) shows, we included weight of fish, seawater temperature, smolt-age and year-class as fixed effects to control for possible confounding (Fig. 2). The coefficient of the main explanatory variable of interest -treatment method- will thus be interpreted as the conditional total effect on the outcome variable (ΔTGC) at any given level of the other fixed effects, whereas the coefficients of the confounding variables are interpreted differently (Westreich and Greenland, 2013). For temperature, for example, the coefficient in Table 4 is interpreted as the controlled direct effect of temperature on the outcome when treatment method is held fixed at a given level. This blocks the temperature effect on treatment method. Similar interpretation is valid for the coefficients of the variables fish weight, year-class and smolt-age.

The descriptive statistics showed, as expected, that treating Atlantic salmon against salmon lice or AGD had a negative effect on the daily change in growth rate (Fig. 1A). Overall, the decrease in growth rate lasted about seven days, as the median of fish groups were back to baseline growth rate (ΔTGC = 0) seven days after a treatment event (Fig. 1A). It took longer for the non-medicinally treated fish-groups (Fig. 1C-D) to return to base-level growth rate compared to medicinally treated groups (Fig. 1B). The descriptive statistics also indicated a great variation in the daily change in growth the week after treatment (Fig. 1A-D). The statistical analysis and post hoc pairwise comparison between treatments showed some of this variance was explained by treatment method, and there was a significant negative effect on growth when treated non-medicinally or with freshwater bath compared to treatments with hydrogen peroxide, medicinal or combination medicinal bath (Table 4).

Stress and injuries caused by both handling and the treatment method itself, might be one explanation for the reduction in growth rate after all treatment methods. The variation both between and within treatment methods, could be explained by differences in the handling procedures associated with treatments. These procedures include length of crowding time, pumping equipment, type of well-boat and thermal/mechanical treatment rig. One explanation for the significantly larger negative effect of non-medicinal treatments could be that these treatments were stressful and caused injuries. This is supported by previous studies and reports from the field that indicate both injuries, increased mortality and decreased resistance to infections after especially thermal and mechanical treatments (Hjeltnes et al., 2018; Overton et al., 2018; Persson et al., 2022; Sviland Walde et al., 2021). Fig. 1A also showed a great variation in the daily change in growth specifically the second day after a treatment. This might be explained by some treatment events extending into day two, instead of ending on day one. Alternatively, there can be different feeding strategies between companies and sites.

Sea temperature and fish weight are adjusted for in the calculation of TGC to make it feasible with growth comparisons between fish groups in both space and time. However, the sea temperature or fish weight may itself be associated with the outcome variable. In the final model, seawater temperature had a statistically significant positive effect on the outcome after a treatment event, implying a greater reduction in growth rate after treatments at lower temperatures relative to treatments at higher temperatures. In regards to thermal treatments, there will be a higher difference between the temperature in the treatment chamber and in the sea if the seawater temperature is low. A higher delta temperature could lead to a larger temperature shock. This could be more stressful for the fish, since exposing Atlantic salmon to warm water lead to aversive reactions and injuries (Gismervik et al., 2019; Moltumyr et al., 2021; Nilsson et al., 2019; Overton et al., 2018). The possible additional stress of thermally treating at lower seawater temperatures could explain decreased growth at low seawater temperatures. Another explanation could be additional stress caused by a higher risk of secondary infections with *Moritella viscosa* and *Tenacibaculum* spp. in injuries caused by handling and treatment (especially mechanical treatment) as the wound healing process takes longer at lower seawater temperatures (Andrews et al., 2015; Sommerset et al., 2020).

The statistical analysis also showed an increasing negative effect on growth rate as the fish grows. This could be due to the increased force necessary to lift and transport the fish in the treatment rig, and thereby increased force on the fish itself or some treatment methods simply were not suitable for larger fish. Another explanation could be an accumulating effect of several management operations during the production. It is also shown that freshwater treatment of salmon <1 kg was associated with higher mortality compared to freshwater treatment of salmon >1 kg (Sviland Walde et al., 2021). Thus, treatments performed at different temperatures and weight at treatment might give different effects on growth after treatment.

Seawater temperature and fish weight could also have an effect on the choice of the treatment method. It is for example preferable to avoid treatments with hydrogen peroxide at high seawater temperatures, and mechanical treatments at low seawater temperatures (Anonymous, 2020; Veterinærkatalogen, 2022).

The variable year-class served as a proxy for time, and thus reflected the shift from medicinal to non-medicinal treatments, and development in treatment methods. The significantly negative effect of the 2015 year-class compared to the 2014 year-class, might be explained by the introduction of and shift to non-medicinal treatment methods. However, the statistical analysis showed this negative effect was reduced over time. The same trend was observed in Sviland Walde et al., 2021, where the median value and the variation in mortality after thermal treatment methods was reduced over the year-classes (Sviland Walde et al., 2021). An explanation for the reduction of this negative effect over the year-classes might be improvements of the non-medicinal treatment methods over time.

Regarding the smolt-age, there are essential differences between a 0 and 1-yearling, for example time and size of stocking. It was therefore biological sensible to adjust for smolt-age in the model.

4.3. *Sources of variation*

Most of the unexplained variation in the statistical model was attributed to individual treatment events (58.8%) and treatments performed close in time at a site (36.7%). Little variation was found between different sites (Table 4). This suggests that change in growth after a treatment event was influenced primarily by factors affecting the individual treatment event (e.g., weather conditions, crowding, management of the delousing unit) and factors affecting the fish-groups within a site equal in time (for example environmental conditions or disease status). This further indicated that timing of the treatment and treatment type was of importance for the growth rate after a treatment. We therefore suggest that future studies, with aims of investigating risk factors for the outcome from lice treatments, should gather high-resolution data within the period of treatment describing fish-group characteristics (such as health-status), environment, handling (such as crowding time), in cage or well-boat treatment, chamber temperature with regards to thermal treatment, and management.

4.4. *Calculating losses in grams*

The estimated adjusted means from treatment method from the mixed effect linear regression model showed a potential short-term loss in weight gain of 52 ± 7.5 g per fish seven days after an individual non-medicinal treatment event compared to a non-treated fish (Table 5). In addition to the lost growth potential caused by the treatment, the pre-treatment starvation period causes a reduction in the growth potential that should be considered when assessing the total effect of treatments on growth. In this study, when including a seven-day period of starvation, 75% of the loss in weight gain was due to the starvation period. The recommended period of starvation for a 3–4 kg salmonid at a seawater temperature of 10 °C is 3–4 days (Anonymous, 2020). In this dataset, the median and average number of starvation days prior to a treatment event, was six days. However, this was based on a cut-off value at maximum seven days of starvation even though some fish-groups in the dataset were starved more than seven days, as we regarded starvation period lasting longer than seven days as unintended. (Anonymous, 2020). Even though the main share of the potential biomass-loss was due to starvation, the period of suboptimal growth the week after treatment was also an important contributor to the overall loss. The estimations in this study was based on feed amount and appetite, and did not include loss of biomass during starvation or a possible negative effect on feed conversion (Einen et al., 1998). The estimation was thus a conservative estimate of the short-term effect of an individual treatment on growth.

Even though the median part of the fish-groups showed a reduction in growth rate that lasted about seven days post treatment, some fish-groups had a positive ΔTGC seven days after treatment (Fig. 1A-D). One possible reason for this could be overfeeding, but it could also indicate increased appetite or compensatory growth. We did not have the ability to investigate the long-term effect on end-harvest weight, since we did not have harvest data. Even though there was quite a substantial loss in potential growth after treatment, Atlantic salmon have great potential to catch up lost growth if they have the time to recover (Hvas et al., 2022). In our study, starvation followed by a non-medicinal treatment reduced the potential weight gain on average by 208 g per fish in a 14-day period. For the fish-groups that experience less than two weeks between treatments, the reduction in weight gain would probably be larger. The number of days between treatments during the production cycle was a median of 38 days and average of 55 days between two treatments. From the last treatment until harvest, there was a median of 54 days and mean of 80 days. Within the first two weeks after an individual treatment, the median part of the fish groups did not show signs of an increased growth rate compared to the growth rate before treatment, $\Delta TGC > 0$ (Fig. 1A-D). In a study by Hvas et al., 2022, it was shown after about 3 months of refeeding and growing at a temperature range of 10-16 °C the size gap of 544 g between a fish group starved eight weeks, and the control group were minor (Hvas et al., 2022). Thus, it seems possible that the main part of the fish-groups in our study did not have enough time between treatments (average four treatments during the production cycle) and after last treatment until harvest, to compensate for the growth loss. In addition, other factors affecting appetite and growth such as disease may extend the required time for full compensatory growth. Further studies are needed to investigate the long-term effect of delousing treatments on growth and the extent of compensatory growth between delousing treatments, in addition to the effect treatment might have on bFCR.

In this paper, we have demonstrated how the estimates from the model can be transformed to calculate the potential weight gain loss in grams/fish of one specific treatment, at one specific time. Assuming the fish did not compensate for the lost growth, this would mean a potential extra biomass of 31,200 kg per cage per non-medicinal treatment, if it was possible to avoid this one non-medicinal treatment. If a site contained five cages (average in this dataset), this would add up to 156,000 kg biomass per site per non-medicinal treatment. In support of this, a recent study shows the mean harvesting weight has decreased since 2012, which corresponds with the onset of the current non-medicinal delousing methods (Barrett et al., 2022).

Results from this study could further be included when modelling economic costs of different strategies to combat salmon lice in the aquaculture industry.

5. Conclusion

In this study, the immediate effect of delousing operations on growth of Atlantic salmon post treatment has been estimated. This was achieved by using daily production data on cage level. The results suggest that all treatment methods reduce growth rate seven days after treatment, where thermal and mechanical treatments have a significantly larger negative effect on growth rate compared to medicinal treatments. The results further indicate that timing of the treatment and treatment type is of importance for the growth rate after treatment. If the number of delousing operations, especially non-medicinal operations, could be reduced, this study indicate a potential for an increased growth and a more efficient aquaculture industry.

Data availability statement

Data are subjected to third party restrictions.

Declaration of Competing Interest

Jostein Mulder Pettersen is affiliated with Pharmaq AS, a pharmaceutical company supplying products to salmon production. Magnus Vikan Røsæg is affiliated with SalMar Farming AS, a Norwegian salmon producer.

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

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2022.738720.

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Paper III

The Economics of Preventing, Replacing or Improving Current Methods for Delousing Farmed Atlantic salmon in Norway

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1. Introduction

There are considerable concerns regarding the sustainability of Norwegian aquaculture of Atlantic salmon, limiting growth in a highly profitable industry (Osmundsen, Olsen, Gauteplass, & Asche, 2022; Sikveland, Tveterås, & Zhang, 2022). Impacts of salmon lice is one of the main concerns and is now the defining element of the regulatory system in terms of whether production will increase, remain constant or decline in each of 13 production areas (Osmundsen, Olsen, & Thorvaldsen, 2020). The prevalence of salmon lice as well as prevention and treatment incur significant costs (Abolofia, Wilen, & Asche, 2017).

Salmon aquaculture production takes 2 ½-3 years from hatching of eggs until harvest. The fish spend the first 10-16 months of their life in a land-based freshwater facility. Subsequently, groups of 150 000- 200 000 salmon are transferred and stocked in open net-cages at seawater sites for an on-growing period for the remaining 14-22 months until harvest. Fish transferred to sea in the fall the same year they hatch are commonly referred to as 0-yearling, while fish transferred the spring the year after they hatched are referred to as 1-yearling. Since production at sea occur in open net cages, the salmon are exposed to seasonal environmental changes such as fluctuating water temperatures, light and salinity, in addition to different pathogens in the water column, including salmon lice.

Following its commercial breakthrough in the early 1970s, salmon farming has developed rapidly from a small-scale production to a large-scale intensive production operated by multi-national companies (Asche, Eggert, Oglend, Roheim, & Smith, 2022). This is partly due to a number of innovations that has reduced production cost and improved competitiveness (Afewerki, Asche, Misund, Thorvaldsen, & Tveteras; Asche, 2008) and increased the scale of each site (Asche, Roll, Sandvold, Sørvig, & Zhang, 2013), as well as dynamic regulatory system that has facilitated this growth (Hersoug, 2021).

As in other biological production processes, salmon aquaculture is affected by different diseases. Many of the diseases are detrimental to salmon aquaculture production as they reduce growth rates and in worst case induce mortality, thereby reducing health and welfare, increasing production cost and reducing profitability (Iversen, Asche, Hermansen, & Nystøyl, 2020). However, production losses also create economic incentives to prevent or treat the diseases, and a rapidly increasing knowledge base has improved the industry's ability to do so (Afewerki et al.).

As production has increased, so has the salmon biomass along the Norwegian coast, which in turn has increased the number of hosts for different pathogens, causing a challenge to the salmon industry itself as well as an externality to wild salmon occupying the same waters (Dean, Aldrin, Qviller, Helgesen, Jansen, & Bang Jensen, 2021). The most important challenge is the ectoparasite salmon lice, *Lepeoptheirus salmonis,* which due to its effect on wild salmon is the main factor in the regulatory system in terms of determining the industry's production growth (Osmundsen et al., 2020).The regulations of lice in farmed salmonids aim to protect both the farmed salmon and reduce the spill-over effect of infestation to wild stocks

(Jeong, Arriagada, & Revie, 2023; NDF, 2012). In Norway, salmon producers are obliged by law to maintain lice levels below a legal maximum limit (NDF, 2012). If the number of lice increases beyond the salmon's ability to compensate, it can cause pathology and eventually death (Pike & Wadsworth, 1999).

For many years, the infestation pressure of lice was kept under control by different medicinal feed or bath treatments. However, during 2000-2012 the lice developed resistance against most of these active substances (Myhre Jensen, Horsberg, Sevatdal, & Helgesen, 2020). From 2015, the dominating treatment practice thus shifted from medicinal treatments to non-medicinal treatments involving heated baths (thermal treatment) and flushing or brushing the lice of the fish (mechanical treatment) (Overton, Dempster, Oppedal, Kristiansen, Gismervik, & Stien, 2018). While there are several options for prevention, such as cleaner fish, semi closed and submerged cages, geographical management etc., there is usually a need for one or several immediate treatments (L. T. Barrett, Oppedal, Robinson, & Dempster, 2020). Currently, the control of salmon lice consists of a mixture of several different preventive measures and immediate treatments, mostly non-medicinal.

An important part of the salmon lice challenge is high mortality due to handling and subsequent treatment of the salmon, especially in the last period of the on-growing phase at sea (Aunsmo, Persson, Stormoen, Romstad, Jamtøy, & Midtlyng, 2023; Bang Jensen, Qviller, & Toft, 2020; Oliveira, Dean, Qviller, Kirkeby, & Bang Jensen, 2021; Overton et al., 2018; Persson, Nødtvedt, Aunsmo, & Stormoen, 2022; Pincinato, Asche, Bleie, Skrudland, & Stormoen, 2021; Sviland Walde, Bang Jensen, Pettersen, & Stormoen, 2021; Tvete, Aldrin, & Jensen, 2023). The salmon lice challenge has led to an increase in handling and subsequent delousing of the salmon (Myhre Jensen et al., 2020). The mortality experience after the non-medicinal treatment methods is shown to be many times higher compared to the medicinal treatment methods (Sviland Walde et al., 2021).

Another important part of the salmon lice challenge is the lost growth potential of the farmed salmon due to starvation prior to treatment and appetite drop after treatment (Walde, Stormoen, Pettersen, Persson, Røsæg, & Bang Jensen, 2022), and it has been argued that the focus on lice in the regulatory system and treatments against salmon lice are some of the reasons for the observed declining size at harvest in Norwegian salmon aquaculture (L. Barrett, Oldham, Kristiansen, Oppedal, & Stien, 2022; Oglend & Soini, 2020).

The increase in mortality and decrease in fish growth affects the profitability of the farmer as it reduces production (Abolofia et al., 2017). However, there is a large variability in the experienced mortality after different delousing treatments, and the effect on growth can vary substantially between the different delousing treatments (Sviland Walde et al., 2021; Walde et al., 2022). The uncertain effect on mortality and growth from a delousing treatment can therefore make it hard for a farmer to decide which control measure to apply to keep the levels of lice below the legal maximum limit.

The objective of the present study is to describe the impact on profits over a single production cycle of salmon, from either 1) preventing treatments; 2) replacing treatments with other treatment methods; or 3) improving treatments by reducing mortality and increasing growth.

2. Material and methods

2.1 Bio-economic modelling

In the present study we apply a stochastic partial budgeting approach. Partial budgeting is a well-known economic tool to support decision-making processes in different areas of animal production (Aunsmo, Valle, Sandberg, Midtlyng, & Bruheim, 2010; Pettersen, Brynildsrud, Huseby, Rich, Aunsmo, Bang, & Aldrin, 2016; Pettersen, Rich, Jensen, & Aunsmo, 2015; Rushton, 2009). This tool quantifies the economic consequences of a specific change in the production procedure by comparing the negative and positive impacts to find the economic net benefit of the change. This analysis does not describe the profitability of a production cycle, but rather how profits are affected by choice of treatment method against salmon lice.

For the partial budgeting analysis we applied a bio-economic model that consisted of several scenarios, where a scenario was defined as the comparison of a single production cycle of either a 1 or 0-yearling with different delousing treatment regimes. The biological input variables were based on distributions from two datasets, one describing mortality and the other describing production and growth of salmon from stocking until harvest. The biological output variables from the simulated production cycles and economic input variables were used to calculate the economic positive and negative impacts of changing a treatment regime. The main output of interest was the economic net benefit of a scenario, expressed as the change in profit.

The bioeconomic model was built in Excel (Microsoft Corporation) with the Monte Carlo simulation add-in tool @Risk (Palisade Corporation, NY, USA) which enables risk analysis by substituting single point estimates of uncertain inputs with distributions sampled randomly by several iterations per simulation.

2.1.1 Data/material

Norwegian salmon farming companies record data of their production, such as number of stocked fish, average fish weight, feeding (type and amount), mortality, treatments, environmental data etc. at the cage-level (NFD, 2008). The dataset in this study is based on daily data from three large Norwegian Atlantic salmon farming companies (companies operating more than 20 sites), and has previously been applied in Walde et al. 2021 (dataset I) and Walde et al 2022 (dataset II). The dataset includes cage-level historical production data related to production and salmon lice treatments.

The dataset applied in Walde et al 2021 describe estimated distributions of change in mortality rate after 4 644 delousing operations. This change was calculated by subtracting the mortality rate seven days after delousing with the mortality rate seven days before delousing. In the current study an additional 165 treatments were excluded from the dataset described in Walde et al 2021 due to missing values for change in mortality rate seven days after treatment. The final dataset I consisted of 4 479 treatments of 1 756 fish-groups from four year-classes, 2014-2017, and 158 sites. The estimated distributions of change in mortality rate (Δmortrate) stratified on treatment method was used as stochastic input variable in the bio-economic model.

Walde et al 2022 estimated the short-term effect of different delousing methods on growth. The dataset applied in this study contained the same source of data as the one applied in Walde et al 2021, however only fish-groups that were possible to trace from stocking until harvest were included. The growth rate was expressed as the thermal growth coefficient (TGC) (Cho, 1992). This was calculated by subtracting the seven day mean of daily TGC after delousing by the five day mean of daily TGC before delousing. In the current study, an additional five fish-groups were excluded due to production length shorter than 200 days. In addition, 21 fish-groups only had treatments against amoebic gill disease (AGD) during the production cycle, and these were also excluded. The final dataset II consisted of 609 fish-groups, 302 1-yearlings and 307 0-yearlings. These came from four year-classes, 2014-2017, and 94 different sites. They were treated a total of 2 281 times. The estimated distributions of change in average daily growth rate (ΔTGC) stratified on treatment method was used as stochastic input variable in the bio-economic model in addition to other biological variables describing production.

2.1.2 Delousing treatments

The treatment methods used were thermal, mechanical, hydrogen peroxide bath, freshwater bath and medicinal bath. Table 1 shows the different categories applied and number of delousing operations within each category.

Table 1 Categorization (n=5) of the immediate treatment operations of farmed Atlantic salmon in three Norwegian companies from 2014-2019.

Categories of treatment operations	**Description of category of delousing operation**
Thermal	Non-medicinal treatment using heated seawater. Includes all treatments using: a. Optilice ® b. Thermolicer c. Heated seawater

Mechanical	Non-medicinal treatment using brushing or flushing. Includes all treatments using: a. FLS Avlusersystem b. Hydrolicer c. SkaMik d. Flushing or mechanical treatment
Hydrogen peroxide	Hydrogen peroxide (H2O2) bath in cage or well boat against salmon lice
Freshwater bath	Freshwater bath in cage or well boat against salmon lice
Medicinal bath	Medicinal bath in cage or well boat using one of the following active substances: a. Azametiphos b. Cypermethrin c. Deltamethrin d. Imidaclorid e. Other f. Cohorts treated with two different combinations of active substances a-f or hydrogen peroxide and one of the active substances a-f

2.1.3 Biological input parameters

The biological input variables in the model were: number of stocked salmon, weight when stocked, month of stocking, length of production, baseline monthly mortality (%), baseline monthly growth rate, average monthly temperature, biological feed conversion ratio (bFCR), days of starvation prior to treatment and change in mortality- and growth rate seven days after different delousing operations (table 2).

The input values for change in mortality (Δmortrate) and growth (ΔTGC) was made stochastic by representing these inputs as distributions (table 2). This was done by applying the observations of Δmortrate (dataset I) and ΔTGC (dataset II) for each treatment method. Distributions for Δmortrate and ΔTGC were fitted based on the observations using the function "Fit" in @Risk. The distribution fit with the lowest Akaike information criterion value was preferred. To avoid unreasonable values and heavy tails, each distribution was truncated at the minimum and maximum values in the respective datasets after the distributions were fitted. Correlation between the input variables Δmortrate and ΔTGC (n= 2 281) was checked using the "correlate" command in Stata (StataCorp, 2017). The distributions were sampled randomly by 10 000 iterations per simulation.

The value for the deterministic biological input variables; number stocked, weight at stocking, month of stocking, length of production and days of starvation were chosen based on descriptive statistics of dataset II. Either the mean, median or mode value was selected as the deterministic input value for each of these variables, based on which value was considered most representative of the underlying distribution. The average monthly temperature was estimated by averaging the monthly temperatures for observations in year 2017 and 2018. The 1-yearlings had a mean stocking weight of 133 grams and the 0-yearlings of 109 grams. In the model, the stocking weight for both smolt types was set to 100 grams for ease of comparison of the two smolt types. The baseline mortality percent ($mort_{baseline}$) and growth rate ($TGC_{baseline}$) defined mortality and growth in months without treatments. The mean growth rate from stocking until first treatment was close to normally distributed, with a mean of 2.9. However, the value of 2.8 was chosen as the baseline in the model to ensure that harvested weight between both smolt types was within the same weight category. The biological feed conversion (bFCR) ratio varied according to the inbound weight of the fish each month. All the monetary values were recorded as Norwegian kroner (NOK), but converted to Euro (€), where 1 € = 10.104 NOK (yearly average 2022).

Table 2 Overview of the variables used in partial budget model. The variables are equal for both 0 and 1-yearling unless otherwise is specified. D=deterministic, S=stochastic. All prices are expressed as 2022-NOK.

Variable	**Data**	**Source**	**Type**	**Distribution**
Number of stocked	150 000	Dataset II	D	-
Production days	488	Dataset II	D	-
Weight at stocking	100g	Dataset II	D	-
Month of stocking 1-yearling/0-yearling	April/August	Dataset II	D	-
Temp per month (ºC)	Jan.=6.2, Feb.=5.1, March=4.2, April=5.2, May=8.2, June=9.9, July=12.0, Aug=14.7, Sept= 13,9, Oct=12.3, Nov=9.8, Dec=7.5	Dataset II	D	-
Days of increased mortality/decreased growth after treatment	7	Dataset II	D	-
Baseline monthly mortality	0.2%	Oliveira et al. (2021)	D	-
Baseline monthly growth	2.8	Dataset II	D	-
Days of starvation prior treatment	5	Dataset II	D	-
Biological feed conversion ratio (bFCR)	Skretting's Relative Growth Index Table	(readimage.aspx (skrettingguidelines .com)	D	-
Change in mortality rate after treatment		*Dataset I Sviland Walde et al. (2021)*	*S*	
Thermal	0.000766			Laplace Truncated (-0.0169, 0.0347)
Mechanical	0.000646			Loglogistic Truncated (0.0075, 0.0706)
Hydrogen peroxide	0.000727			Loglogistic Truncated (-0.0054, 0.0637)
Freshwater	0.0000905			Loglogistic

				Truncated (-0.0032, 0.0265)
Medicinal	0.0000105			Laplace Truncated (-0.0054, 0.0266)
Change in growth rate after treatment		*Dataset II* *Walde et al. (2022)*	*S*	
Thermal	-0.95581			Normal Truncated (-3.9846, 2.9028)
Mechanical	-0.92332			Logistic Truncated(-3.5377, 1.8403)
Hydrogen peroxide	-0.56656			Logistic Truncated(-3.4213, 1.8779)
Freshwater	-0.88385			Pert Truncated (-2.6792, 1.1462)
Medicinal	-0.36908			Logistic Truncated (-3.7493, 4.3831)
Feed prices	14.60 NOK/kg dryfeed	Intrafish.no Ilaks.no	D	-
Handling dead cost	2.12 NOK/kg round weight	Pettersen et al. (2015)	D	-
Harvesting cost	4.05 NOK/kg round weight	(Pettersen et al., 2015)	D	-
Treatment cost	NOK/kg live weight		D	-
Thermal	0.37	Iversen, Hermansen, Nystøl, and Junge Hess (2017)		
Mechanical	0.26	Iversen et al. (2017)		
Hydrogen peroxide	0.50	Iversen et al. (2017)		
Freshwater	1.33	Iversen et al. (2017)		
Medicinal	0.37	Iversen et al. (2017)		
Sales price per weight class	NOK/kg head on gutted (HOG) week 47, 2022	NASDAQ NASDAQ Salmon Index (nasdaqomxtrader.com)	D	-
3-4	76.53			
4-5	79.90			
5-6	85.72			
6-7	96.00			
7-8	99.31			
8-9	100.86			
9+	101.99			

2.1.4 *Biological output parameters*

The biological output parameters from the different production cycles were the harvested weight (eq. 1.1) and biomass (1.5), and accumulated amount of feed used (eq. 1.6) at the end of each production cycle.

The weight gain in a non-treatment month was calculated by setting the TGC in eq. 1.3 equal to TGC $_{baseline}$ the entire period of the month. The weight gain (wg_t) during a treatment month was calculated in three steps:

1) During starvation ($wg_{t\ starv}$): A treatment is initiated by a starvation period. During this period, the TGC in eq. 1.3 would be equal to zero, thus the weight gain ($wg_{t\ starv}$) would also be zero.

2) Post treatment ($wg_{t\ post\ treat}$): The weight gain seven days (t=7) after a treatment ($wg_{t\ post\ treat}$) was calculated by substituting TGC in eq. 1.3 with $TGC_{post\ treat}$ (eq. 1.4).

3) For the remaining part of the month ($wg_{t\ rem}$): After the starvation and post treatment period (t=14), the weight gain in the remaining part of the month ($wg_{t\ rem}$) was calculated by setting the TGC in eq. 1.3 equal to the $TGC_{baseline}$ and t= number of remaining days within the treatment month. This implies an assumption of no compensatory growth after a treatment.

(eq. 1.1)

$$weight_{harvest} = weight_{stocking} + \sum_{T=1}^{n=17} (wg_{\ t\ starv} + wg_{\ t\ post\ treat} + wg_{\ t\ rem})$$

(eq. 1.2)

$$weight_{\ T} = weight_{T-1} + wg_{\ t\ starv} + wg_{\ t\ post\ treat} + wg_{\ t\ rem}$$

(eq. 1.3)

$$wg_{\,t} = weight_{t-1} - \left\{ weight_{\,t-1}^{\left(\frac{1}{3}\right)} + \left(\frac{TGC}{1000} * \ temp_T * t\right)^3 \right\}$$

(eq. 1.4)

$$TGC_{post\ treat} = TGC_{baseline} + \Delta TGC$$

T= month, t= days, n=number of months, wg= weight gain, starvation period default = 7 days, post treatment period default = 7 days, temp = average monthly temperature, post treat = post treatment, rem = remaining (weight gain remaining period)

The mortality rate, Δmortrate, was transformed to an incident risk (Toft, Agger, Houe, & Bruun, 2004) and the monthly inbound number of fish (N_T) was calculated by subtracting the baseline mortality and the number of dead seven days after a treatment from the inbound number of fish the previous month (Nt-1) (eq. 1.5). In no-treatment month Δmortrate would be equal to zero. It was assumed that the treatments occurred in the beginning of the month, initiated by the pre-treatment starvation period of five days. This generated a small bias in number of dead, as both the baseline mortality and the treatment mortality was calculated from the inbound number at the start of the month. However, the accumulated effect from four treatments was minor and consistent across all scenarios, and the bias thus regarded of no importance to the modelled outcome.

(eq.1.5)

$$N_T = N_{T-1} - (mort_{baseline} \times N_{T-1}) - \left(N_{T-1} \times e^{-\Delta mortrate \times t}\right)$$

(eq.1.6)

$$aB = \sum_{T=1}^{n=17} (N_T \times weight_T)$$

aB= accumulated biomass, n=number of months

(eq.1.7)

$$aFeed = \sum_{T=1}^{n=17} \left(\frac{wg_T}{1000} \times bFCR\right) N_T$$

aFeed= accumulated amount of feed in kg, bFCR= biological feed conversion ratio

(eq.1.8)

$$aBDead = \sum_{T=1}^{n=17} \left[weight_T \left((mort_{baseline} \times N_T) + \left(N_T \times e^{-\Delta mortrate \times t}\right)\right)\right]$$

aBDead= accumulated biomass of dead, n=number of months

(eq.1.9)

$$aBTreat = \sum_{T=1}^{n} (weight_T \times N_T)$$

aBTreat = accumulated treated biomass, n = number of treatments

2.1.5 Economic input parameters

The price components in the model were: feed (p_{feed}) handling of dead fish, (p_{mort}), harvesting, (p_{harv}), and treatment (p_{treat}) (table 2). The feed prices were expressed as NOK/ per kg dry feed. The handling of dead fish and harvesting prices were expressed as NOK/ per kg produced round weight (Pettersen et al., 2015). Price of different treatment methods per kg treated fish (p_{treat}) were obtained from Iversen et al. (2017). These estimates included the cost of mortality per kg treated fish, and were equal for thermal, mechanical and freshwater treatments, 0.17 NOK/kg treated. The cost of mortality was subtracted from these numbers since treatment specific mortality was retrieved from dataset I (table 2). All the prices were adjusted for inflation to 2022 NOK using the monthly consumer price index reported by Statistics Norway. The price increase from 2015 and 2017 to 2022 was 22.8% and 16.4%, respectively.

Since the objective was to estimate the economic benefit ($\Delta\Pi$) of a change, only variable costs from delousing operations were included in the model and it was assumed that fixed costs would not change between different treatment methods or production cycles of same length.

Salmon prices for different weight classes were provided from Nasdaq (NASDAQ Salmon Index (nasdaqomxtrader.com)). The Nasdaq Salmon indices consists of 11 individual price indices for weekly reported sales prices of Norwegian farmed salmon of the highest quality classification called superior quality (table 2). Nine of the indices are prices for nine different weight categories (1-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9 and 9+ kilograms), while the other two are weighted average prices across all, or a selection of the most sold (3-6 kilos), weight categories. In the model, the sales price (p) was made dependent on harvested weight, using the Nasdaq price categories for different weight categories. The spot sales prices for week 47, 2022 was used as input in the model (Table 2).

2.1.6 Economic output parameters

The cost of handling dead fish (M_{cost}), harvesting cost (H_{cost}), feed cost (F_{cost}) and treatment cost (T_{cost}) were calculated by eq. 1.10-1.13. The harvested weight and biomass, and accumulated biomass of dead fish was converted to head on gutted (HOG) or round weight as appropriate, by using a conversion factor of 1.067 or 1.2, respectively (NDF, 2019). The main output variable of interest, the difference in profit ($\Delta\Pi$) (eq. 1.14) was calculated for each scenario.

(eq.1.10)

$$M_{cost} = \frac{aDead}{1.07} \times p_{mort}$$

(eq.1.11)

$$H_{cost} = \frac{aB}{1.07} \times p_{harv}$$

(eq.1.12)

$$F_{cost} = aFeed \times p_{feed}$$

(eq.1.13)

$$T_{cost} = aT \times p_{treat}$$

(eq. 1.14)

$$\Delta\Pi_{scen\,n} = \left\{\left(\mathrm{p} \times \frac{\mathrm{aB}}{1.2}\right) - \left(M_{cost} + \mathrm{H}_{\mathrm{cost}} + F_{cost} + T_{cost}\right)\right\}_{prod\,x} - \left\{\left(\mathrm{p} \times \frac{\mathrm{aB}}{1.2}\right) - \left(\mathrm{M}_{\mathrm{cost}} + \mathrm{H}_{\mathrm{cost}} + F_{cost} + \mathrm{T}_{\mathrm{cost}}\right)\right\}_{prod\,y}$$

Scen=scenario, n=scenario number, prod=production cycle

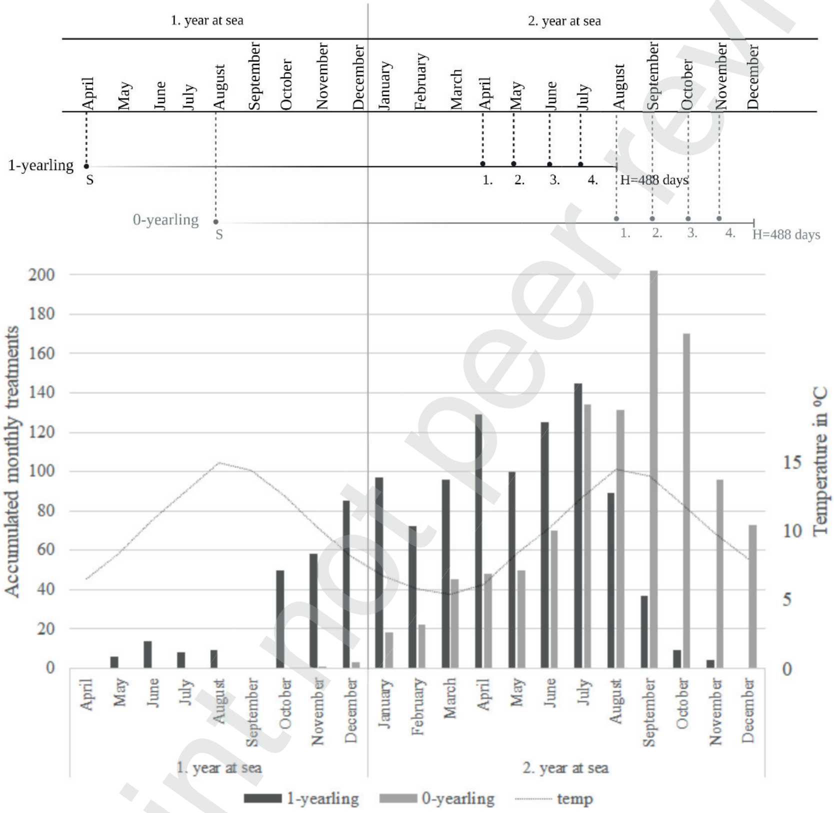
We assumed the entire harvested biomass to be “superior”, the harvested weight of each fish within the fish-group to be the same as the average weight of the fish-group, and the weight of the dead fish to be the same as the average weight of the fish-group the month of death. We further assumed that the (bFCR) was not affected by the treatments.

2.1.7 Modelled production cycle and baseline treatment regime

The number of treatments during a production cycle, when they occurred, the time elapsed between treatments and the type of treatments was defined as a treatment regime. The treatment regime was selected by descriptive statistics of dataset II. In dataset II, the most common type of treatment in the recent year classes (2016 and 2017) was thermal treatments, and the fish groups were on average treated four times during the production cycle. For both smolt types, half of all treatments were performed 20-40 days apart, and number of days from last treatment until harvest was positively skewed with a mode of 31 days. The occurrence of the treatments, however, differed between the smolt types (figure 1). The temperature ranged from the lowest temperature in March of 5.3ºC to a peak in August of 14.4ºC. The highest occurrence of treatments for the 1-yearling is in April (n=129) and for the 0-yearling in September (n=202).

The selected baseline treatment regime in the model was therefore four thermal treatments that occurred in the second year in sea for both smolt types (Figure 1). The 1-yearling was treated in April, May, June and July and harvested one month later (Figure 1). The 0-yearling was treated in August, September, October and November and harvested one month later (Figure 1). The production at sea lasted for 488 days for both smolt types, and both were treated for the first time 365 days after stocking. The weight of the 1-yearling ranged from 2.5 kg-3.4kg and for the 0-yearling 2.3 –3.8 kg in the treatment months.

Figure 1 shows the modelled production cycle of the two smolt types with month of stocking (S), treatment months (numerated 1 to 4), month of harvest (H), and the monthly occurrence of treatments in dataset II, to show how the seasonal change in temperature in Celsius degrees (dotted line) and the accumulated occurrence of treatments for the two smolt (bar graph) is incorporated in the model. Created with BioRender.com



2.1.8 Scenarios

A production cycle with the baseline treatment regime was compared with a production cycle where one or several of the thermal treatments were either prevented, replaced or improved.

In scenario 1 the baseline treatment regime was compared with a production cycle without treatments. In addition, we also compared four mechanical treatments to a production cycle without treatments (scenario 2). In scenario 3 and 4, two out of four thermal treatments were prevented, either the first and second or the third and fourth. In scenario 5 and 6 one out of four thermal treatments was prevented, either the first or the fourth. In scenario 7-10 the first thermal treatment was replaced with either a mechanical (scenario 7), hydrogen peroxide (scenario 8), freshwater (scenario 9) or medicinal bath (scenario 10). In scenario 11-13 we looked at the variance in profit if four thermal treatments were within the 5% worst performing treatments with respect to mortality and growth of the salmon, compared to an expected performance (scenario 11), expected compared to 5% best (scenario 12) and 5% worst compared to 5% best (scenario 13). Altogether, this created 13 different scenarios listed in table 3.

Table 3 The different scenarios (n=13) for both 1 and 0-yearling.

	Description of scenario	Scenario number
Prevent	4/4 thermal treatments*	1
	4/4 mechanical treatments*	2
	first two (2/4) thermal treatments**	3
	last two (2/4) thermal treatments**	4
	first (1/4) thermal treatment**	5
	last (1/4) thermal treatment**	6
Replace	first (1/4) thermal treatment with one mechanical treatment**	7
	first (1/4) thermal treatment with one hydrogen peroxide bath**	8
	first (1/4) thermal treatment with one freshwater bath**	9
	first (1/4) thermal treatment with one medicinal bath**	10

Improve	4/4 thermal treatments from 5% worst-> expected	11
	4/4 thermal treatments from expected -> 5% best	12
	4/4 thermal treatments from 5% worst -> 5% best	13

*Compared to production without treatments

**Compared to production with four thermal treatments (scenario 1).

2.2 Sensitivity analysis

To assess the effect from varying the values of the deterministic input variables on the output value, sensitivity analyses were performed on the following input variables: baseline growth rate, baseline mortality, days of starvation, and feed and sales prices. The range of the low and high input values for the variables in the sensitivity analyses was based on the descriptive statistics of dataset II and literature. Baseline growth rate was assumed to be normally distributed in the sensitivity analysis, with 5th and 95th percentiles set to 2.3 and 3.2 for TGC. Monthly mortality was assumed a uniform distribution with a minimum of 0.1 and a maximum 1.0%. Days of starvation had a uniform distribution with minimum four and maximum seven days of starvation. Feed prices were assumed a triangular distribution with +/- 20% min/max, and sales prices were assumed a triangular distribution with +/- 40% min/max. The regression coefficients of the input variables were compared in a Tornado chart by applying the function for sensitivity analysis in @Risk.

In dataset I and II, there were <14 observations of thermal treatments in the year 2014. We suspected that these might have an effect on the expected output, as the mortality after these treatments was quite high. We therefore compared the output with and without these observations.

3. Results

2.3 The economic benefit (ΔΠ) of changing delousing treatment regime

For all scenarios, except scenario 9, the most important driver for the expected economic benefit of a change in treatment regime, is the increase in revenue, followed by increased feed costs in scenario 1-6 (table 4). For scenario 9 (replacing a thermal treatment with a freshwater treatment), the increase in treatment cost is the most important driver.

The change in profit for most measures are slightly higher for the 0-yearling compared to the 1-yearling (table 4).

The economic benefit of changing the delousing treatment regime varies, especially regarding the prevention of four thermal treatment (figure 2).

Table 4 shows the expected total change in costs, revenue and profit for the different scenarios in Euro (€). Scenario 11-13 are not included as they reflect the variance in scenario 1. A negative sign indicates a decrease in cost or revenue.

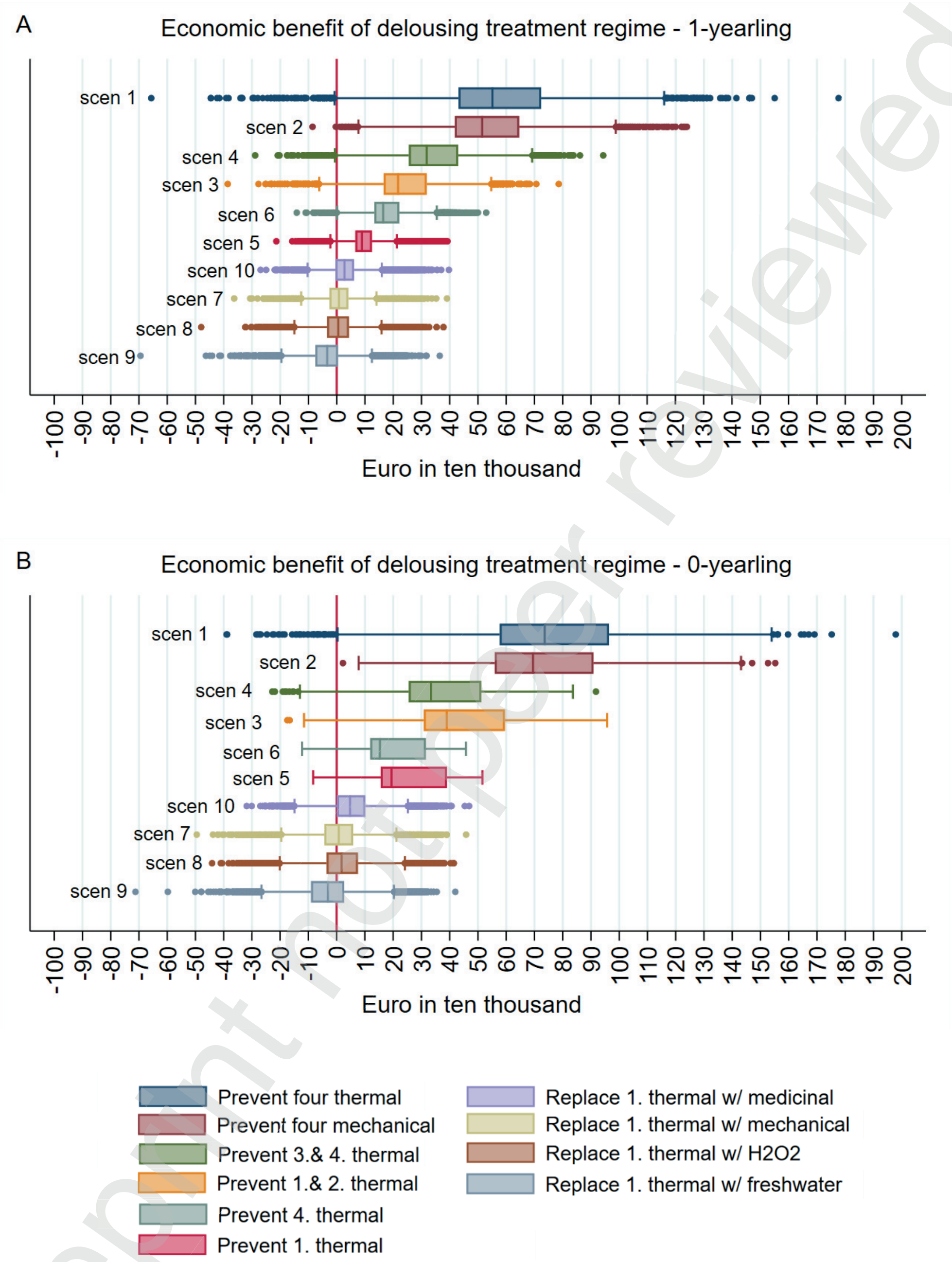
€ total	1-yearling									
Scenario no	1	2	3	4	5	6	7	8	9	10
Costs										
Feed	152 708	150 369	60 445	94 835	26 151	49 003	574	2 005	- 137	5 117
Treatment	- 53 552	- 43 588	- 22 427	- 29 272	- 10 702	- 8 828	- 2 165	6 725	37 154	2 171

Slaugther	38 244	37 073	14 741	22 541	5 966	12 068	265	538	- 175	1 946
Mortality	- 1 839	- 1 542	- 749	- 849	- 354	- 549	- 63	- 15	74	- 339
Revenue	670 874	650 322	258 585	395 409	104 647	211 696	4 650	9 446	- 3 070	34 134
Profit *(ΔΠ)*	535 313	508 011	206 574	308 153	83 586	160 002	6 039	193	- 39 985	25 239

€ total	0-yearling									
Scenario no	1	2	3	4	5	6	7	8	9	10
Costs										
Feed	211 795	209 332	121 728	83 367	62 284	35 665	819	5 360	526	10 008
Treatment	- 57 460	- 46 790	- 20 271	- 33 231	- 8 073	- 17 682	- 1 991	6 440	34 570	2 335
Slaugther	51 066	49 804	28 217	21 170	14 365	9 641	334	1 388	- 15	3 222
Mortality	- 1 959	- 1 636	- 663	- 1 160	- 254	- 620	- 61	- 5	75	- 322
Revenue	895 786	873 654	494 974	371 364	251 981	169 119	5 851	24 353	- 271	56 518
Profit *(ΔΠ)*	692 346	662 944	365 963	301 218	183 659	142 115	6 751	11 169	- 35 426	41 275

The measures ranged by positive economic benefit are prevention, improvement and replacement.

Figure 2 shows the variance in profit change for the 1-yearling (A) and 0-yearling (B) measured in ten thousand € per cage per production cycle. The scenarios are ranged by the median increase in profit for the 1-yearling. The red reference line indicates no change in profit by changing delousing regime. A positive change in profit indicates a positive economic impact of changing delousing regime.



2.3.1 Prevention

The model does not include the direct costs of various preventive measures because of the uncertain effect on reduction in number of immediate treatments as well as the direct costs. The economic benefit would therefore indicate how much a farmer could use on preventive measures per cage before it is no longer economical beneficial. Preventing or avoiding thermal and mechanical treatments has a large expected economic positive benefit (table 4, scenario 1-6). For instance is the expected increase in profit by preventing four thermal treatments 535 313€ per cage per production cycle for a 1-yearling and 692 346 for a 0-yearling (table 4).

For 1-yearlings, preventing the last or two last treatments (scenario 6 and 4) have a greater effect than preventing the first or two first treatments (scenario 5 and 3) (table 4 and figure 2). For the 0-yearling, this is opposite; preventing the first or two first treatments have a greater effect than preventing the last or two last treatments (table 4).

2.3.2 Replacement

For both smolt types, replacing the first thermal treatment with another treatment measure has a minor expected economic positive benefit, compared to the other measures of preventing or improving (table 4, scenario 7-10). In fact, replacing a thermal treatment with a freshwater treatment (scenario 9) has an expected negative benefit (table 4).

Table 4 shows, that for the 1-yearling replacing the first thermal treatment with a mechanical treatment has a greater positive impact compared to replacing it with a hydrogen peroxide treatment. This is the opposite for the 0-yearling where replacing the thermal treatment with a hydrogen peroxide treatment has a greater positive impact on profit change compared to replacing it with a mechanical treatment.

2.3.3 Improvement

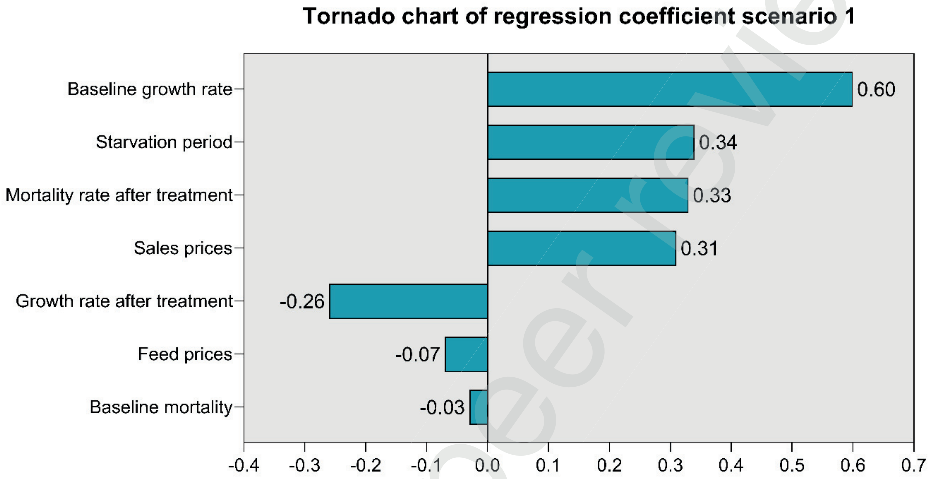
The direct cost of improving treatments is not included in the model, thus the economic benefit of improving indicates what could be spent per cage per production cycle before break even. Improving treatments have a high economic impact, especially if the farmer is able to improve the baseline treatment regime of four thermal treatments from being among the 5% worst to the 5% best performing (figure 2 and supplementary table). The economic benefit of improving four treatments from the 5% worst to expected, expected to 5% best and from worst to best performing has an economic benefit of 319 196, 418 738 and 737 934 €/cage for a 1-yearling and 355 761, 476 703 and 832 464 €/cage for a 0-yearling (supplementary table, scenario 11-13).

2.1 Sensitivity analysis

The sensitivity analysis of the input variables; baseline growth rate ($TGC_{baseline)}$, baseline mortality ($mort_{baseline),}$ mortality rate after treatment (Δmortrate), growth rate after treatment (ΔTGC), starvation period, sales price and feed price, shows that for scenario 1-6 the model is most sensitive to baseline growth rate and the length of the starvation period (scenario1, 2, 4, 5) following mortality rate after treatment or sales prices dependent on the scenario (figure 3) The economic loss increases with increasing baseline TGC, starvation period and sales prices. For all scenarios, decrease or increase in baseline mortality and feed prices are of lesser importance. The most important factor in scenario 6-10 is the treatment mortality, followed by the growth rate after treatment.

Removing the 14 thermal treatments from 2014 had no effect on the simulated output, they were therefore kept in the distribution.

Figure 3 Tornado plot of sensitivity analysis showing the ranking of the regression coefficient of the selected input variables comparing four thermal treatments (baseline) to a production cycle without treatments (scenario 1).



4. Discussion

The results suggest that accounting for the biological losses associated with lice treatments is important when making choices of delousing strategies. The biological costs of increased mortality and decreased growth associated with especially non-medicinal treatments are expected to be high, but varies substantially. Therefore, the economic benefit of preventing or improving can also be high. Salmon producers could thus invest a considerable amount in measures for prevention or improvement of thermal treatments before break-even. Replacing one thermal treatment with another immediate treatment method has a minor effect. The results further shows that sales value and feed consumption constitutes the largest share of the change in profit between the scenarios.

Feed and sales prices are the two most important drivers for the outcome of a change in treatment regime. The increased revenue is due to decreased mortality and increased growth, which means harvesting more and larger salmon. The increased harvest weight might also shift more salmon into a higher weight class, thus extra price premium will give additional revenue. As feed constitutes about 50% of the production costs (Iversen et al., 2020; Misund, Oglend, & Pincinato, 2017), most of the increased production cost when preventing treatments is due to increased total amount of feed used in the production cycle. This increase is explained by avoiding periods of pre-treatment starvation and decreased appetite after treatment. In addition, mortality after treatments is avoided, thus a larger number of fish needs to be fed. The cost of harvesting and handling of dead fish are minor compared to feed and sales prices, and do not affect the profit change to the same degree as feed costs and revenue.

Overall, the economic benefit for the different scenarios is higher for the 0-yearling compared to the 1-yearling (table 4). This can be explained by higher seawater temperatures in the treatment months for the 0-yearling (9.4-14.7 ºC) compared to the 1-yearling (5.2-12.0 ºC) (figure 1). Preventing treatments thus leads to a larger reduction in growth loss for the 0-yearling compared to the 1-yearling, which ultimately leads to a difference in harvested biomass. The model accordingly indicates that preventing treatments in the months with the highest seawater temperatures, would be more beneficial than preventing treatments in months with lower temperatures, because the potential growth loss is reduced. However, an exception to this general observation has been reported for thermal treatments, in which sea water temperatures in the lower ranges are associated with negative impact on growth rates, possibly due to the larger interval between treatment- and sea water temperature (Walde et al., 2022). The pressure of lice is higher in the months with higher seawater temperatures, thus treatments in these months could be harder to avoid. In addition, mechanical treatments at low seawater temperatures are associated with a higher risk of winter-wounds (Andrews, Stormoen, Schmidt-Posthaus, Wahli, & Midtlyng, 2015; Sommerset, Sviland Walde, Wiik-Nielsen, Bornø, Oliveira, Haukaas, & Brun, 2022). The model does not account for the possible interaction between growth rate and temperature, nor increased risk of secondary diseases.

Not surprisingly, preventing all four non-medicinal treatments, especially poorly executed thermal treatments, has the largest economic benefit (table 4, scenario 1-2). A recent study demonstrated that combining different preventive measures could reduce the number of delousing events by 25% during a production cycle (Oldham, Simensen, Trengereid, & Oppedal, 2023). In our study, this would be equivalent to preventing one thermal treatment. Table 4 shows that if preventing the first thermal treatment (scenario 5) a farmer could justify using 83 586 (1-yearling) or 183 659 (0-yearling) €/cage, as long as the preventive measures do not affect the mortality nor the growth of the salmon.

In Iversen et al. (2017) the cost of a thermal treatment is estimated to be 0.054 € per kg salmon treated, including a mortality cost of 0,017 € per kg treated. However, in their estimations the economic value of a dead salmon is equal to the production cost per kg, whereas in our estimations the cost of mortality also includes opportunity cost associated with revenue loss, in addition to growth loss which would be equivalent to 0.14-0.30€/kg. This shows that not including the risk of mortality and growth loss associated with delousing treatments, in addition to the alternative cost of lost revenue could lead to underestimating the cost of a thermal treatment.

In practice, it is challenging to prevent all treatments during a production cycle, and the current control of delousing normally consists of a mixture of preventive and immediate treatment measures (L. T. Barrett et al., 2020). Scenario 11-13 (supplementary table) highlights the importance of improving the quality of thermal treatments, showing the greatest potential effect on profits comes from improving from the 5% worst to the 5% best performing treatments. However, the direct cost of improving treatments is not included in the model because there is little research done identifying potential risk factors related to increased mortality and decreased growth after thermal and mechanical delousing. As in the case of prevention, the model therefore indicates what could be spent per cage per production cycle on improving the treatments. Regarding the thermal treatments, the model shows that it would be economical justifiable to use up to 740 000 €/cage (1-yearling) or 830 000 €/cage (0-yearling) (supplementary table, scenario 13) to improve four poor performing thermal treatments to be among the best performing. Thus, there exists an substantial economic incentive for prioritising research on identifying factors related to issues such as handling procedures, the treatment rig, prior health status of the fish, and timing of the treatment, etc. to improve thermal treatments by reducing mortality and ensuring good growth after treatment.

Replacing one thermal treatment with other treatments such as mechanical, hydrogen peroxide, medicinal bath or freshwater bath has a minor effect economic benefit. For instance, replacing one thermal treatment with one freshwater treatment has a negative net benefit. The reason for this is that the direct cost of freshwater treatments are much higher compared to thermal treatments (Iversen et al., 2017), while the impact on mortality and growth is approximately the same. However, alternating between different treatments is an important part of an integrated pest management strategy to prevent resistance (Myhre Jensen et al., 2020), and this benefit has not been accounted for in our model. The model also assumes that the effect of removing the salmon lice is the same for all treatments, which would not be the case, especially regarding medicinal treatments due to resistance (Myhre Jensen et al., 2020).

Replacing a thermal with a hydrogen peroxide or mechanical treatment has opposite effects on the two smolt-groups. For the 1-yearling, the harvest weight and biomass are slightly higher in a production where a thermal treatment is replaced by a hydrogen peroxide instead of replacing it with a mechanical treatment. However, the cost of the hydrogen peroxide treatment is greater than a mechanical treatment. This means the gain of increased biomass is outweighed by the cost of the treatment for the 1-yearling. For the 0-yearling, the increased weight gain is larger compared to the 1-yearling when replacing the thermal treatment with a hydrogen peroxide treatment instead of a mechanical treatment. This larger increase in weight gain outweighs the larger cost of hydrogen peroxide bath compared to the cost of a mechanical treatments. This example illustrates the fact that deciding between measures of delousing can be different for the 1-yearling and 0-yearling, and be difficult since direct and indirect costs can turn out to be unequally important to the net economic benefit.

The sensitivity analysis shows that profitability is very sensitive to small changes in baseline growth, suggesting that ensuring good appetite and growth of the salmon during production and treatment is perhaps the most crucial measurement for increasing profits. The model is not very sensitive to changes in baseline mortality. A monthly mortality of less than 1% is defined as non-extreme in a study from 2018 (Overton et al., 2018). Baseline mortality in the model is thus low, and would perhaps affect the model to a greater extent if above 1%. However, if baseline monthly mortality is higher than 1%, the relative importance of treatment mortality would decrease, and there may be other challenges in addition to salmon lice that needed to be prioritised to decrease overall mortality.

We used the year-classes of 2016 and 2017 to choose different treatment scenarios because these were the year-classes closest to reflecting the current treatment regimes. The technical solutions in aquaculture of Atlantic salmon in Norway progresses quickly, and treatment procedures may have improved since 2016-2019. This imply that the current economic benefit might be smaller than stated here, however delousing operations is still regarded as the second most important single cause of mortality (Sommerset et al., 2022)

There are several constraints in this model, some of them already mentioned. For instance is it assumed that no compensatory growth occurs between the treatments, nor can the farmer extend the production length to compensate for the growth loss, since the production length is fixed in the model. In the model, the treatments occur monthly, and it seems realistic to assume that the salmon do not have time to compensate the growth loss between the treatments based on a prior study by Hvas, Nilsson, Vågseth, Nola, Fjelldal, Hansen, Oppedal, Stien, and Folkedal (2022). If the length between the treatments or the time from last treatment until harvest was extended, it might be reasonable to include the possibility of compensatory growth in the model. However, as described in Holan, Roth, Breiland, Kolarveic, Hansen, Iversen, Hermansen, Gjerde, Hatlen, Mortensen, Lein, Johansen, Noble, Gismervik, and Espmark (2017) farmers report minor flexibility for adapting the production, for instance by increasing the production length to compensate for growth loss.

In addition, the model does not account for the fact that the production in Norway is regulated by a maximum allowed biomass (MAB) (Hersoug, 2021). Prolonging the production cycle might also increase the risk of another delousing operation. The production length could be affected if we put a MAB constraint into the model. Farmers normally partially harvest sites to ensure optimal use within the biomass constraint, which might prolong the production time at the site. Since this study is described at the cage level, the MAB constraint was not included, however at a site level this would be relevant. The economic gain of decreasing mortality and increasing growth would also be related to a shorter production time and perhaps more flexibility both in planning the production and having a harvestable weight ready when price is high. This flexibility or real option also has a value, which is not incorporated in this bio-economic model.

Although the present model is a simplification, by comparing one choice with an alternative, it catches some of the complex dynamic between the indirect (biological) costs, direct costs and environmental factors (temperature). It also reflects the fact that some of the choices are not very intuitive. An example of this could be in the case when the benefits of increased growth and decreased mortality are only slight and thus outweighed by the cost of implementing the measure for doing so. It is apparent that no single model can, nor should, implement the whole complexity of the production of Atlantic salmon with all its risk and uncertainty. However, there is a need for both simple and more complex bio-economic models that incorporates risk and uncertainty by the use of high-resolution production data and epidemiological research to aid well founded decisions.

Salmon lice has become a complex, political and expensive problem. It is central to the public regulation of the growth of salmon aquaculture industry in Norway, and influence many parts of the on-growing production and planning of the production of Atlantic salmon at sea (NDF, 2012, 2017, 2022). Several studies have shown the enormous monetary cost associated with salmon lice, and thus highlighted the importance of prioritising the problem both at a macro and microeconomic level (Abolofia et al., 2017; Costello, 2009; Iversen et al., 2020; Liu & Bjelland, 2014; Mustafa, Rankaduwa, & Campbell, 2001; Olaussen, Liu, & Skonhoft, 2015). Salmon lice control is a cost to both society, the farmer and the salmon. In addition, there is a cost to the salmon by reduced health and welfare, which manifests as an indirect cost to the farmer in the form of a lower output/biomass. As our model shows, it is important to include the large variance in the indirect costs related to mortality and growth when assessing the economic benefit, as it shows that improving the current non-medicinal treatments have a great positive economic benefit, and therefore identifying risk factors related to improving non-medicinal treatments should be prioritized.

5. Conclusions

This study has investigated the economic benefit of changing between different treatment regimes against salmon lice by using a partial budgeting approach and a unique high-resolution (cage level) dataset that captures the variance in biological losses due to treatments. To the authors knowledge this is the first bio-economic model that incorporates biological risk (mortality and growth) related to delousing treatments using estimated distribution from high-resolution production data.

The study most importantly shows a substantial economic incentive for both preventing and improving the current non-medicinal treatment methods by securing good animal health and welfare. Importantly, it also shows that it is possible to improve factors leading to poorly executed thermal treatment methods.

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mill € (NOK)	1-yearling																									
scenario no	1		2		4		3		6		5		10		8		7		9		11		12		13	
expected	*0.54*	*(5.41)*	*0.51*	*(5.13)*	*0.31*	*(3.11)*	*0.21*	*(2.09)*	*0.16*	*(1.62)*	*0.08*	*(0.84)*	*0.03*	*(0.26)*	*0.00*	*(0.01)*	*0.01*	*(0.06)*	*-0.04*	*(-0.39)*	0.32	(3.23)	0.42	(4.23)	0.74	(7.46)
mean	0.57	(5.78)	0.54	(5.46)	0.35	(3.53)	0.24	(2.47)	0.20	(2.02)	0.11	(1.16)	0.03	(0.35)	0.01	(0.08)	0.01	(0.11)	-0.03	(-0.35)						
median	0.55	(5.57)	0.51	(5.20)	0.32	(3.22)	0.22	(2.19)	0.16	(1.66)	0.09	(0.90)	0.03	(0.28)	0.01	(0.05)	0.01	(0.08)	-0.03	(-0.34)						
5% pct	0.22	(2.18)	0.28	(2.81)	0.14	(1.45)	0.07	(0.68)	0.08	(0.77)	0.02	(0.18)	-0.06	(-0.63)	-0.11	(-1.08)	-0.09	(-0.89)	-0.16	(-1.58)						
95% pct	0.95	(9.64)	0.88	(8.86)	0.62	(6.24)	0.47	(4.79)	0.40	(4.08)	0.30	(3.01)	0.20	(1.99)	0.15	(1.52)	0.12	(1.20)	0.09	(0.89)						
IQR	0.29	(2.96)	0.23	(2.30)	0.17	(1.77)	0.15	(1.54)	0.09	(0.89)	0.06	(0.60)	0.07	(0.67)	0.08	(0.78)	0.07	(0.68)	0.08	(0.81)						
max	1.78	(17.95)	1.24	(12.52)	0.94	(9.53)	0.79	(7.94)	0.53	(5.35)	0.39	(3.96)	0.40	(4.01)	0.38	(3.82)	0.39	(3.95)	0.36	(3.68)						
min	-0.66	(-6.63)	-0.09	(-0.86)	-0.29	(-2.92)	-0.39	(-3.90)	-0.14	(-1.43)	-0.21	(-2.16)	-0.27	(-2.72)	-0.48	(-4.85)	-0.36	(-3.67)	-0.69	(-7.02)						
	0-yearling																									
scenario no	1		2		3		4		5		6		10		8		7		9		11		12		13	
expected	0.69	(7.00)	0.66	(6.69)	0.37	(3.70)	0.30	(3.04)	0.18	(1.86)	0.14	(1.44)	0.04	(0.42)	0.01	(0.12)	0.01	(0.07)	-0.03	(-0.34)	0.36	(3.59)	0.48	(4.82)	0.83	(8.41)
mean	0.76	(7.66)	0.73	(7.34)	0.43	(4.39)	0.37	(3.73)	0.25	(2.53)	0.19	(1.95)	0.06	(0.64)	0.03	(0.27)	0.01	(0.11)	-0.03	(-0.29)						
median	0.74	(7.44)	0.70	(7.02)	0.39	(3.94)	0.33	(3.37)	0.19	(1.96)	0.15	(1.55)	0.05	(0.48)	0.02	(0.18)	0.01	(0.08)	-0.03	(-0.31)						
5% pct	0.34	(3.40)	0.39	(3.97)	0.19	(1.95)	0.14	(1.43)	0.10	(1.00)	0.06	(0.65)	-0.07	(-0.74)	-0.13	(-1.34)	-0.16	(-1.63)	-0.22	(-2.26)						
95% pct	1.17	(11.81)	1.09	(11.00)	0.69	(6.93)	0.60	(6.08)	0.43	(4.30)	0.37	(3.69)	0.27	(2.74)	0.25	(2.53)	0.23	(2.33)	0.19	(1.95)						
IQR	0.39	(3.91)	0.35	(3.53)	0.29	(2.90)	0.26	(2.60)	0.23	(2.37)	0.20	(1.99)	0.10	(1.02)	0.11	(1.12)	0.10	(1.03)	0.12	(1.19)						
max	1.98	(19.99)	1.55	(15.69)	0.96	(9.67)	0.92	(9.27)	0.52	(5.21)	0.46	(4.63)	0.47	(4.74)	0.41	(4.19)	0.46	(4.63)	0.42	(4.24)						
min	-0.39	(-3.94)	0.02	(0.22)	-0.17	(-1.77)	-0.23	(-2.30)	-0.08	(-0.84)	-0.12	(-1.24)	-0.32	(-3.22)	-0.44	(-4.46)	-0.50	(-5.01)	-0.71	(-7.20)						

Supplementary S1 shows the descriptive statistics of change in profit in million euros (NOK) for the different scenarios. Scenario 11-13 are the variance in scenario 1 between the expected and the 5% lowest values (11), expected and 5% highest values (12), and 5% lowest and 5% highest values (13).

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